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On the cover: *Paravaejovis pumilis* (Williams, 1980), ♂.
Photo by R. Mercurio.

Redefinition and Generic Revision of the North American Vaejovid Scorpion Subfamily Syntropinae Kraepelin, 1905, with Descriptions of Six New Genera

Edmundo González-Santillán
and Lorenzo Prendini

Bulletin of the American Museum of Natural History

REDEFINITION AND GENERIC REVISION OF THE NORTH AMERICAN VAEJOVID SCORPION SUBFAMILY SYNTROPINAE KRAEPELIN, 1905, WITH DESCRIPTIONS OF SIX NEW GENERA

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ABSTRACT

The endemic North American vaejovid scorpion subfamily Syntropinae Kraepelin, 1905, is redefined and its component genera revised, based on a simultaneous phylogenetic analysis of 250 morphological characters and 4221 aligned DNA nucleotides from three mitochondrial and two nuclear gene markers. Tribe Stahnkeini Soleglad and Fet, 2006, is removed from Syntropinae. Tribe Paravaejovini Soleglad and Fet, 2008, and subtribe Thorelliina Soleglad and Fet, 2008, are abolished: Paravaejovini Soleglad and Fet, 2008 = Syntropinae Kraepelin, 1905, syn. nov.; Thorelliina Soleglad and Fet, 2008 = Syntropinae Kraepelin, 1905, syn. nov. Eleven genera, six newly described, are recognized within Syntropinae: *Balsateres*, gen. nov.; *Chihuahuanus*, gen. nov.; *Kochius* Soleglad and Fet, 2008; *Konetontli*, gen. nov.; *Kuarapu* Francke and Ponce-Saavedra, 2010; *Maaykuyak*, gen. nov.; *Mesomexovis*, gen. nov.; *Paravaejovis* Williams, 1980; *Syntropis* Kraepelin, 1900; *Thorellius* Soleglad and Fet, 2008; *Vizcaino*, gen. nov. *Hoffmannius* Soleglad and Fet, 2008, is abolished: *Hoffmannius* Soleglad and Fet, 2008 = *Paravaejovis* Williams, 1980, syn. nov. *Lissovaejovis* Ponce-Saavedra and Beutelspacher, 2001 [nomen nudum] = *Paravaejovis* Williams, 1980, syn. nov. Ten species, formerly placed in *Hoffmannius*, are transferred to *Paravaejovis*: *Paravaejovis confusus* (Stahnke, 1940), comb. nov.; *Paravaejovis diazi* (Williams, 1970), comb. nov.; *Paravaejovis eusthenura* (Wood, 1863), comb. nov.; *Paravaejovis flavus* (Banks, 1900), comb. nov. [nomen dubium]; *Paravaejovis galbus* (Williams, 1970), comb. nov.; *Paravaejovis gravicaudus* (Williams, 1970), comb. nov.; *Paravaejovis hoffmanni* (Williams, 1970), comb. nov.; *Paravaejovis puritanus* (Gertsch, 1958), comb. nov.; *Paravaejovis spinigerus* (Wood, 1863), comb. nov.; *Paravaejovis waeringi* (Williams, 1970), comb. nov. *Paravaejovis schwenkmeyeri* (Williams, 1970), comb. nov., is removed from synonymy. Four species, formerly placed in *Kochius*, are transferred to *Chihuahuanus*, gen. nov.: *Chihuahuanus cazieri* (Williams, 1968), comb. nov.; *Chihuahuanus crassimanus* (Pocock, 1898), comb. nov.; *Chihuahuanus kovariki* (Soleglad and Fet, 2008), comb. nov.; *Chihuahuanus russelli* (Williams, 1971), comb. nov. Four species, formerly placed in *Kochius*, *Thorellius*, or *Vaejovis* C.L. Koch, 1836, are transferred to *Mesomexovis*, gen. nov.: *Mesomexovis atenango* (Francke and González-Santillán, 2007), comb. nov.; *Mesomexovis oaxaca* (Santibáñez-López and Sissom, 2010), comb. nov.; *Mesomexovis occidentalis* (Hoffmann, 1931), comb. nov.; *Mesomexovis subcristatus* (Pocock, 1898), comb. nov. *Mesomexovis variegatus* (Pocock, 1898), comb. nov., is reinstated to its original rank as species. Four subspecies are newly elevated to species: *Kochius barbatus* (Williams, 1971), stat. nov.; *Kochius cerralvensis* (Williams, 1971), stat. nov.; *Kochius villosus* (Williams, 1971), stat. nov.; *Mesomexovis spadix* (Hoffmann, 1931), comb. et stat. nov. Three subspecies are synonymized: *Vaejovis diazi transmontanus* Williams, 1970 = *Paravaejovis diazi* (Williams, 1970), syn. nov.; *Vaejovis bruneus loretoensis* Williams, 1971 = *Kochius villosus* (Williams, 1971), syn. nov.; *Vaejovis hoffmanni fuscus* Williams, 1970 = *Paravaejovis hoffmanni* (Williams, 1970), syn. nov.

INTRODUCTION

The North American vaejovid scorpion subfamily Syntropinae Kraepelin, 1905, as redefined in the present contribution, is a morphologically and ecologically diverse group of scorpions (fig. 1) that includes some of the largest and most robust vaejovids, reaching lengths of 94 mm, and some of the smallest, at 14 mm. Syntropinae are endemic to North America, extending from Oregon and Utah in the southwestern United States to the Isthmus of Tehuantepec in Chiapas and Oaxaca, Mexico, and occur in a variety of habitats including sand dunes and rocky desert, subtropical deciduous forest, and pine-oak forest, from sea level to more than 3500 m altitude (table 1, figs. 2–6). Like other vaejovids, many Syntropinae are substratum specialists (Prendini, 2001a), inhabiting substrata within a limited range of hardness and composition for which they display ecomorphological adaptations (Williams, 1987; Polis, 1990). Lithophilous, lapidicolous, and psammophilous ecomorphotypes are all represented in the subfamily (fig. 1). Consequently, many Syntropinae are endemic to particular geological formations (e.g., isolated mountain ranges and sand systems), and occupy restricted distributional ranges (Williams, 1980).

The taxonomic history of Syntropinae, discussed further below, is inextricably linked to that of the family Vaejovidae Thorell,

Fig. 1. Representative species in the North American vaejovid scorpion subfamily Syntropinae Kraepelin, 1905. **A.** *Chihuahuanus bilineatus* (Pocock, 1898), comb. nov., ♀; **B.** *Kochius bruneus* (Williams, 1970), ♂; **C.** *Mesomexovis punctatus* (Karsch, 1879), comb. nov., ♂; **D.** *Syntropis macrura* Kraepelin, 1900, ♀; **E.** *Thorellius* sp., ♂; **F.** *Vizcaino viscainensis* (Williams, 1970), comb. nov., ♂. Photos in **B**, **D** and **E** courtesy of R. Mercurio.

1876, the generic composition of which has undergone considerable modification since first proposed (Thorell, 1876; Laurie, 1896; Pocock, 1893; Kraepelin, 1905; Stahnke, 1974; Francke and Soleglad, 1981; Sissom, 1990, 2000; Stockwell, 1992; Soleglad and Fet, 2003, 2005, 2006, 2008; Graham and Soleglad, 2007; Francke and Ponce-Saavedra, 2010). Vaejovidae is currently restricted to North American taxa, but its monophyly and composition, like that of its component genera and suprageneric taxa, was not satisfactorily tested until recently. The only cladistic analyses previously presented (Stockwell,

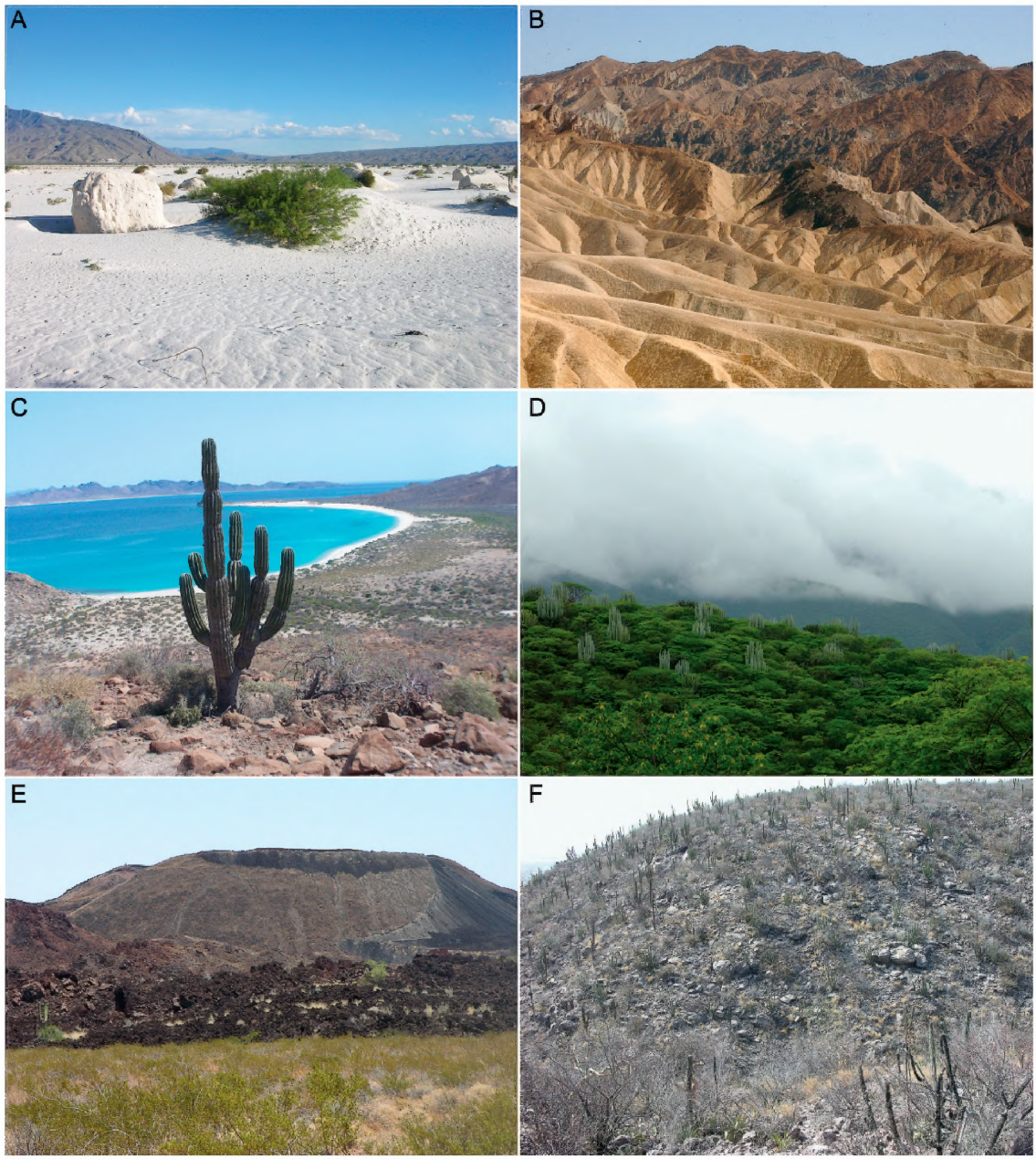


Fig. 2. Representative habitats of species in the North American vaejovid scorpion subfamily Syntropinae Kraepelin, 1905. **A.** Cuatro Cienegas de Carranza, Coahuila, Mexico, habitat of *Chihuahuanus cazieri* (Williams, 1968), comb. nov., *Chihuahuanus coahuilae* (Williams, 1968), comb. nov., and *Chihuahuanus globosus* (Borelli, 1915), comb. nov. **B.** Death Valley, California, habitat of *Kochius hirsuticauda* (Banks, 1910). **C.** Isla Espiritu Santo, La Paz, Baja California Sur, Mexico, habitat of *Kochius insularis* (Williams, 1971), *Paravaejovis diazi* (Williams, 1970), comb. nov., and *Paravaejovis gravicaudus* (Williams, 1970), comb. nov. **D.** Cuicatlán, Oaxaca, Mexico, habitat of *Mesomexovis subcristatus* (Pocock, 1898), comb. nov. **E.** Pinacate desert, Sonora, Mexico, habitat of *Paravaejovis confusus* (Stahnke, 1940), comb. nov. **F.** West of La Paz, Baja California Sur, Mexico, habitat of *Syntropis williamsi* Soleglad et al., 2007. Photos in **B** and **E** courtesy of R. Mercurio and in **C** courtesy of I.G. Nieto.

TABLE 1

Currently recognized genera in the North American vaejovid scorpion subfamily Syntropinae Kraepelin, 1905, with countries, states and geographical regions from which they have been recorded

Abbreviations: Mex. (Mexico): Ags (Aguascalientes), B.C. (Baja California), B.C.S. (Baja California Sur), Chis (Chiapas), Chih. (Chihuahua), Coah. (Coahuila), Col. (Colima), Dgo (Durango), Gto (Guanajuato), Gro (Guerrero), Hgo (Hidalgo), Jal. (Jalisco), Edomex. (Estado de México), Mich. (Michoacán), Mor. (Morelos), Nay. (Nayarit), N.L. (Nuevo León), Oax. (Oaxaca), Pue. (Puebla), Qro (Querétaro), Sin. (Sinaloa), Son. (Sonora), Tamps (Tamaulipas), Tlax. (Tlaxcala), Ver. (Veracruz), Zac. (Zacatecas); U.S.A.: AZ (Arizona), CA (California), NM (New Mexico), NV (Nevada), OR (Oregon), TX (Texas), UT (Utah); Balsas Depression (BD), Baja California Peninsula (BCP), Chihuahuan Desert (CD), Great Basin Desert (GBD), Mojave Desert (MD), Pacific Coast (PC), Sonoran Desert (SD), Trans-Mexican Volcanic Belt (TMVB).

Genus	Country: State	Region
Balsateres, gen. nov.	Mex.: Mich.	BD
Chihuahuanus, gen. nov.	Mex.: Ags, Chih., Coah., Dgo, N.L., Tamps, Zac.; U.S.A.: AZ, NM, TX	CD
Kochius Soleglad and Fet, 2008	Mex.: B.C., B.C.S., Son.; U.S.A.: AZ, CA, NV	BCP, MD, SD
Konetontli, gen. nov.	Mex.: B.C.S., Col., Gro, Jal., Mich., Nay.	BCP, BD, PC
Kuarapu Francke and Ponce-Saavedra, 2010	Mex.: Mich.	BD
Maaykuyak, gen. nov.	Mex.: B.C.S., Chih., Coah., Dgo, N.L.; U.S.A.: TX	BCD, CD
Mesomexovis, gen. nov.	Mex.: Ags, Col., Chis, Gto, Gro, Hgo, Jal., Edomex., Mich., Mor., Nay., Oax., Pue., Qro, Sin., Tlax., Ver., Zac.	BD, PC, TMVB
Paravaejovis Williams, 1980	Mex.: B.C., B.C.S., Chih., Son., Sin.; U.S.A.: AZ, CA, NV, NM, OR, UT	BCP, GBD, MD, SD
Syntropis Kraepelin, 1900	Mex.: B.C., B.C.S.	BCP
Thorellius Soleglad and Fet, 2008	Mex.: Ags, Col., Edomex., Gto, Gro, Jal., Mich., Nay., Sin.	BD, PC
Vizcaino, gen. nov.	Mex.: B.C., B.C.S.	BCP

1989; Soleglad and Fet, 2003), the first of which was never published, the second severely criticized (Prendini and Wheeler, 2005), were based on the same characters and philosophy, and suffer from the same flaws. Both Stockwell (1989) and Soleglad and Fet (2003) employed supraspecific terminals, the monophyly of which was assumed rather than tested (Prendini, 2000, 2001b), and applied a peculiar method of character coding that forced character transformations based on preconceived notions of phylogenetic relationship and/or character evolution (Prendini and Wheeler, 2005). These limitations have been addressed in major reanalyses of vaejovid phylogeny (González-Santillán and Prendini, in press; Prendini et al., in prep.), based on comprehensive taxon sampling with species as terminals, and an extensive dataset of morphological characters and DNA sequences from five markers in the nuclear and mitochondrial genomes. The monophyly and composition of the vaejovid genera and suprageneric taxa were rigorously tested in these analyses and a solid framework for the classification presented. Among other discoveries, the spinose (hooked or toothed) margin of the distal barb (sensu Stockwell, 1989, 1992; figs. 7, 8) of the sclerotized hemimating plug was identified as a unique, unambiguous synapomorphy for Syntropinae, uniting taxa previously assigned to different subfamilies (Soleglad and Fet, 2008) and requiring the redefinition and generic revision presented here.

The present contribution implements the taxonomic discoveries of the simultaneous phylogenetic analysis of 250 morphological characters (205 qualitative and 45 quantitative) and 4221 aligned DNA nucleotides from three mitochondrial and two nuclear gene markers, by González-Santillán and Prendini (in press), which established the monophyly and composition of Syntropinae and its component genera (fig. 7, appendix 1). The diagnosis of the subfamily is revised and

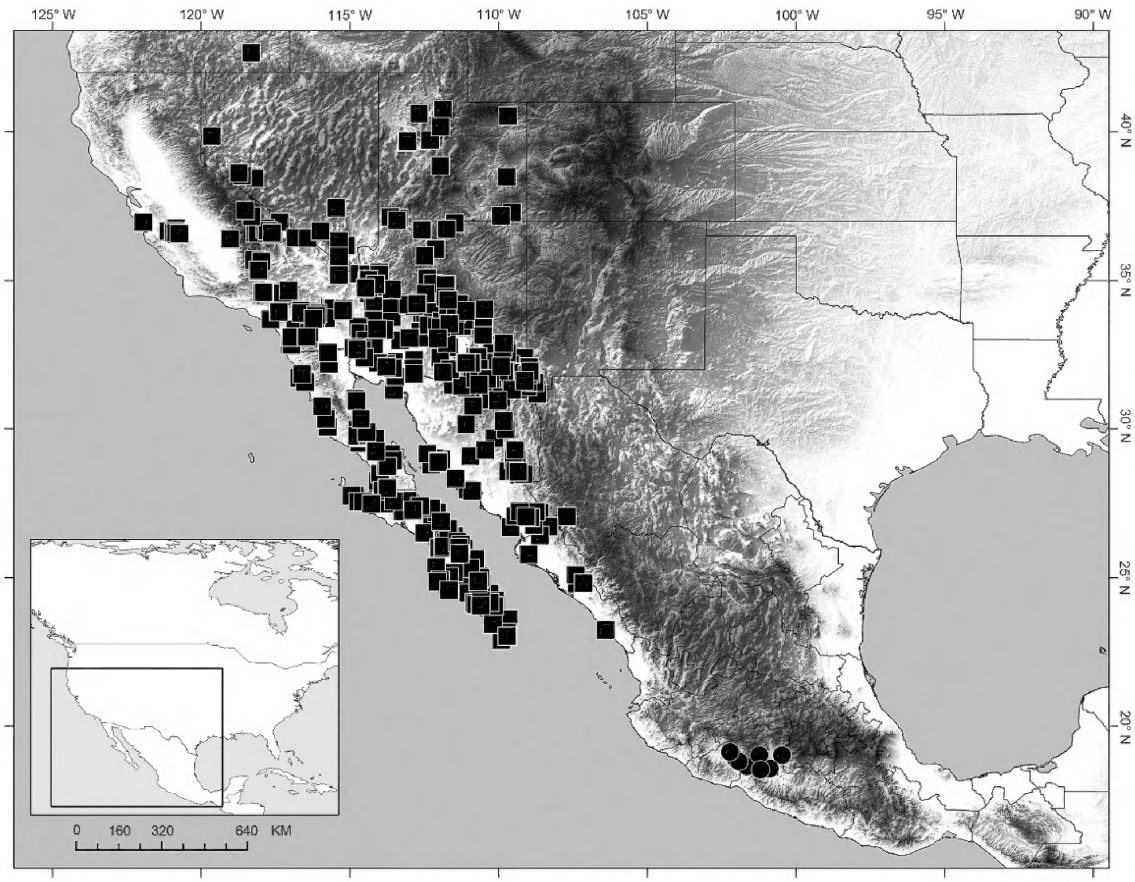


Fig. 3. Map of southwestern North America, plotting known locality records for two genera in the vaejovid scorpion subfamily Syntropinae Kraepelin, 1905, based on data collected in the present study: *Balsateres*, gen. nov. (circles); *Paravaejovis* Williams, 1980 (squares).

tribe Stahnkeini Soleglad and Fet, 2006, removed from it. Tribe Paravaejovini Soleglad and Fet, 2008, and subtribe Thorelliina Soleglad and Fet, 2008, are abolished. *Hoffmannius* Soleglad and Fet, 2008, is abolished, the diagnoses of five genera revised, and six new genera described. A key to the identification of the 11 genera in the subfamily is presented. Twenty-one new combinations are created by transferring species, formerly placed in *Hoffmannius* Soleglad and Fet, 2008, *Kochius* Soleglad and Fet, 2008, *Thorellius* Soleglad and Fet, 2008, or *Vaejovis* C.L. Koch, 1836, to other genera. Three subspecies are synonymized, one species removed from synonymy, four subspecies newly elevated to species and one species reinstated to its original rank.

TAXONOMIC HISTORY OF SYNTROPINAE

Syntropinae was among the first five subfamilies originally recognized in Vaejovidae and was originally created to accommodate the monotypic genus, *Syntropis* Kraepelin, 1900, endemic to the Baja California Peninsula of Mexico, and defined on the presence of a single ventral median carina on metasomal segments I–IV (Kraepelin, 1905). The subfamily remained monotypic for more than 70 years. Subsequent attempts to organize the diversity of taxa presently accommodated within it are recounted below.

Hoffmann (1931) produced the first monograph on Mexican scorpions, in which the genus *Vaejovis* was grouped into three

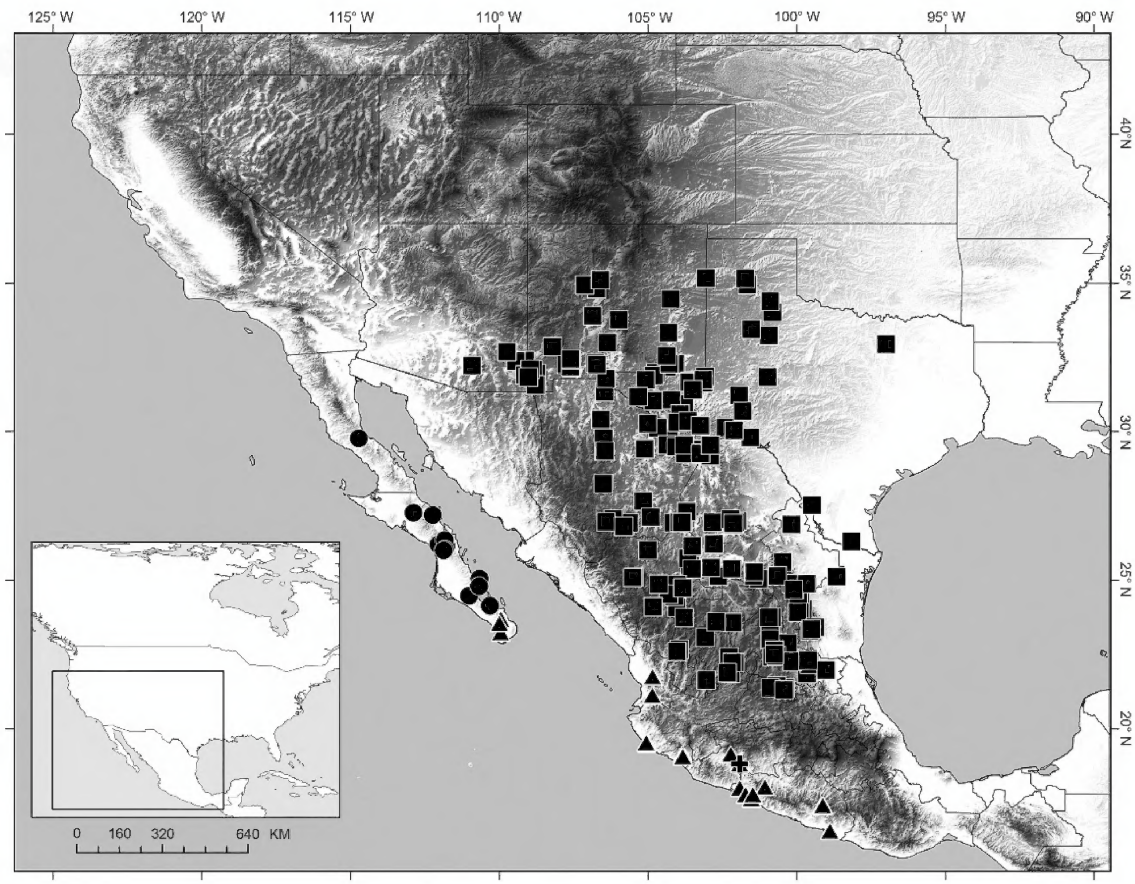


Fig. 4. Map of southwestern North America, plotting known locality records for four genera in the vaejovid scorpion subfamily Syntropinae Kraepelin, 1905, based on data collected in the present study: *Chihuahuanus*, gen. nov. (squares); *Konetontli*, gen. nov. (triangles); *Kuarapu* Francke and Ponce-Saavedra, 2010 (cross); *Syntropis* Kraepelin, 1900 (circles).

"sections." The first and second of Hoffmann's (1931) sections represent the precursors of the *eusthenura* and *intrepidus* groups of *Vaejovis* (Williams, 1970a; Sissom, 1989) that would later become genera presently included within Syntropinae. Hoffmann (1931) separated the two sections on the basis of total body size, extent of carination on the pedipalp chela manus, and presence of granulation on the ventral carinae of the metasomal segments. Hoffmann (1931) studied many specimens from mainland Mexico, but examined little material from northern Mexico and Baja California. However, Williams (1968, 1969, 1970a, 1970b, 1970c, 1971a, 1971b, 1974, 1980) subsequently conducted extensive fieldwork in these areas, using ultraviolet (UV) light detection, resulting in the descriptions of several new genera and species.

Williams (1969) collected new material of *Syntropis* for the first time since its description and added a second species to the genus. Stahnke (1974) created a new genus, *Vejovoidus* Stahnke, 1974, to accommodate Williams' (1969) second species of *Syntropis*, and included both monotypic genera in Syntropinae based on the shared presence of a single ventral median carina on metasomal segments I–IV. Subsequent authors expressed doubts about the validity of the subfamily as defined by Stahnke (1974), arguing that the single ventral median carina probably evolved independently in *Syntropis* and *Vejovoidus* (Soleglad, 1976; Francke, 1981;

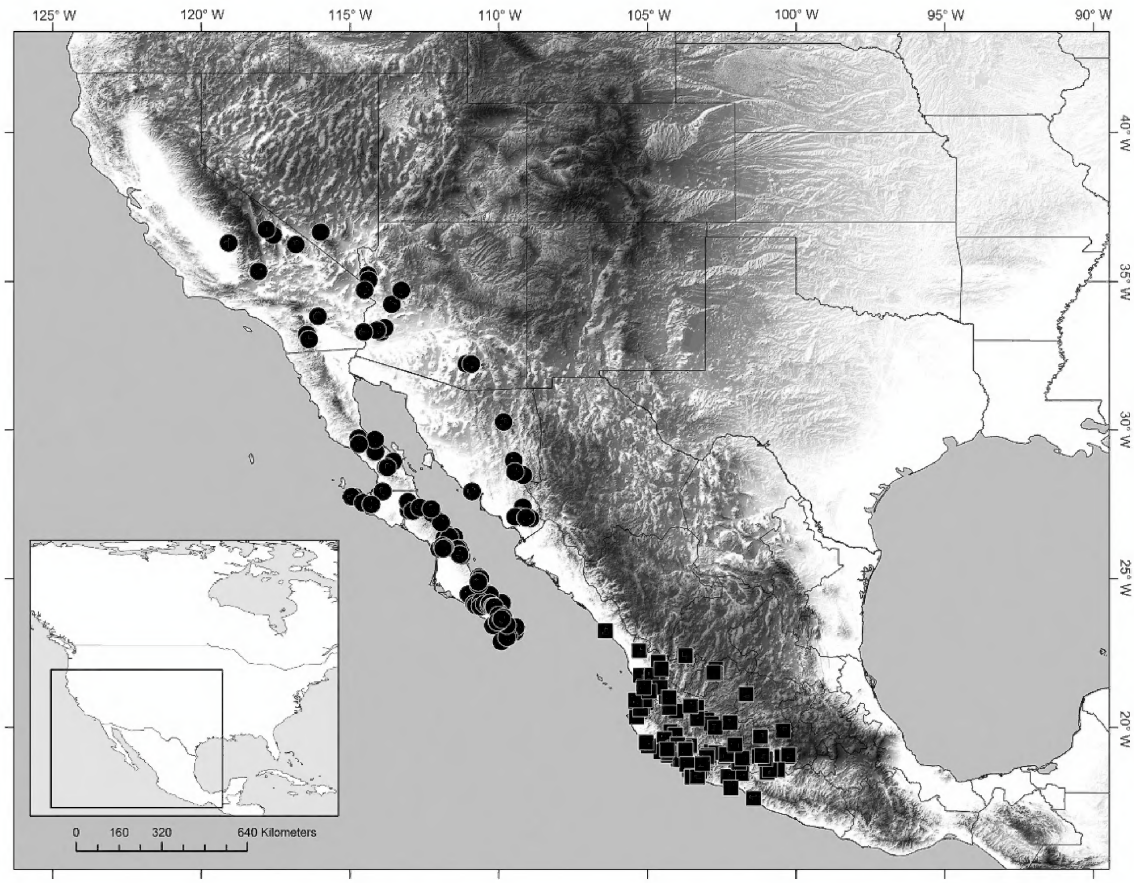


Fig. 5. Map of southwestern North America, plotting known locality records for two genera in the vaejovid scorpion subfamily Syntropinae Kraepelin, 1905, based on data collected in the present study: *Kochius* Soleglad and Fet, 2008 (circles); *Thorellius* Soleglad and Fet, 2008 (squares).

Sissom, 1990), but the subfamily was not dissolved until later (Stockwell, 1992).

Williams (1970a, 1970b, 1971b) proposed several species groups of *Vaejovis*, including the *eusthenura* group, based in part on Hoffmann's (1931) "first section" of *Vaejovis*, and the *punctipalpi* group—two of the most diverse clades to be later incorporated within Syntropinae (tables 2, 3). The *eusthenura* group was characterized by the mostly acarinate pedipalps and ventral surfaces of the metasomal segments, whereas the *punctipalpi* group was characterized by the granular carinae of these segments.

Williams (1980) described *Paravaejovis* Williams, 1980, another monotypic vaejovid genus from Baja California, diagnosed primarily by a neotrichobothriotaxic pedipalp chela, to accommodate a species originally placed in the *pumilis* group of *Vaejovis* (Williams, 1970b, 1970c). Haradon (1983, 1984a, 1984b, 1985) suggested that *Paravaejovis* was more closely related to another vaejovid genus, *Paruroctonus* Werner, 1934, and to the *borregoensis* microgroup of that genus in particular, with which Haradon (1984b) suggested it might be subordinate, based on a suite of characters mostly associated with psammophily. Most subsequent authors accepted the hypothesis that *Paravaejovis* is related to *Paruroctonus* (Sissom, 1990, 2000; Stockwell, 1992; Soleglad and Fet, 2003, 2008) rather than an alternative hypothesis, discussed by Stockwell (1989, 1992) and Soleglad and Fet (2008), that it could be related to *Syntropis* and the *eusthenura*, *intrepidus*, and *punctipalpi* groups of *Vaejovis*, with which it shares a unique character of the hemispermatophore.

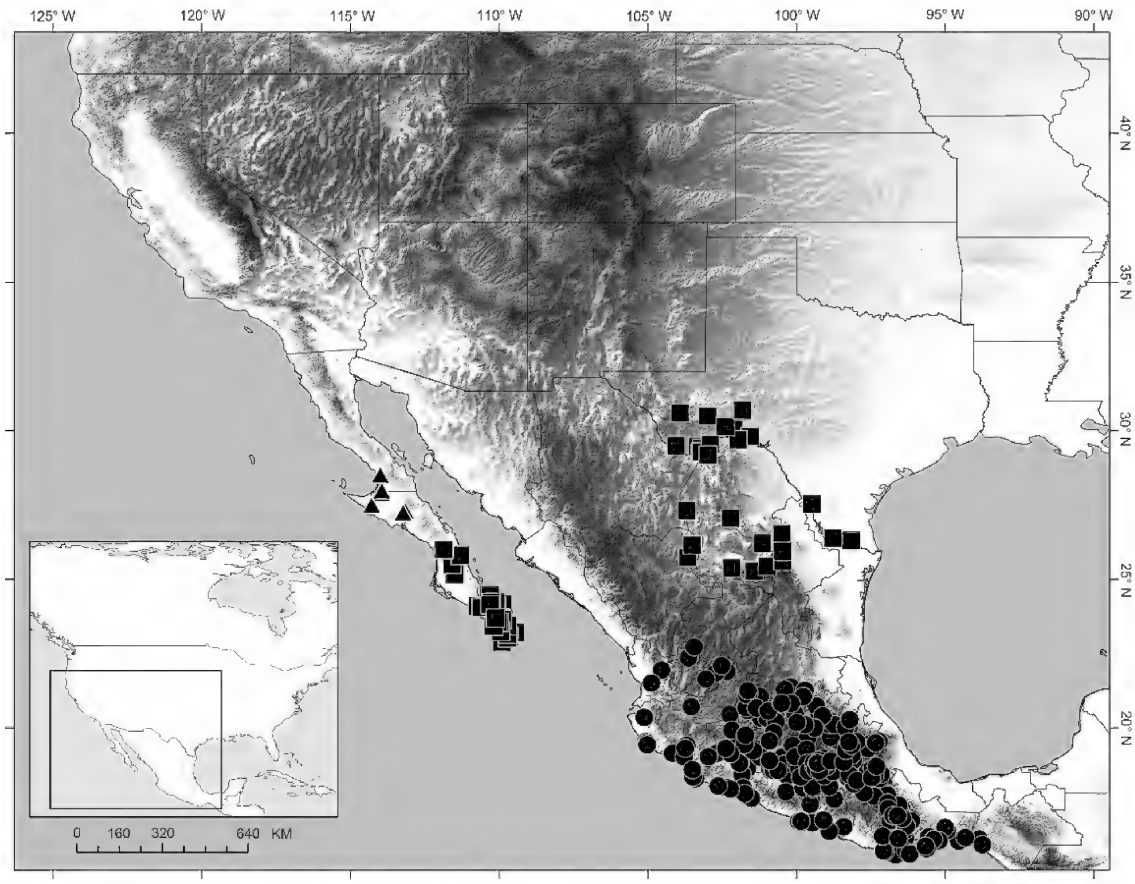


Fig. 6. Map of southwestern North America, plotting known locality records for three genera in the vaejovid scorpion subfamily Syntropinae Kraepelin, 1905, based on data collected in the present study: *Maaykuyak*, gen. nov. (squares); *Mesomexovis*, gen. nov. (circles); *Vizcaino*, gen. nov. (triangles).

By the 1990s, Stockwell (1989, 1992) and Sissom (1990) had identified problems with the genera and species groups of Vaejovidae proposed earlier (Hoffmann, 1931; Williams, 1970a, 1971a; Soleglad, 1973; Sissom and Francke, 1985; Sissom, 1989). Stockwell (1989) presented the first cladistic analysis of the family, based on morphological characters scored for supraspecific terminal taxa representing the vaejovid genera and four of the species groups of *Vaejovis* recognized at the time. Stockwell (1989) proposed a revised suprageneric classification of Vaejovidae (table 2) that included three new genera, formal names for the already well-established *eusthenura*, *nitidulus*, and *punctipalpi* groups of *Vaejovis* (Williams, 1970a, 1971a; Sissom and Francke, 1985).

Stockwell (1992) later published some of his proposed revisions to the classification of Vaejovidae (including the transferal of *Nullibrotheas* Williams, 1974, to Chactidae Pocock, 1893, and the elevation of Scorpiopidae Kraepelin, 1905 [as "Scorpiopsidae"], to the rank of family), but not the new genera or revised suprageneric taxa. Stockwell (1992: 409) synonymized Syntropinae with Vaejovidae, contradicting his earlier decision, and leaving the family without suprageneric taxa, while suggesting that "distinct groupings within this family are clear enough to recognize subfamilies, but I will defer on this subject until a later time." Additionally, Stockwell (1992: 408, 409) noted:

> Among the Vaejovinae, *Syntropis* appears to share at least one potential synapomorphy with the *punctipalpi*, *eusthenura*, and *intrepidus*

> groups of *Vaejovis* Koch, 1836 (i.e., the presence of numerous spines on the margin of the distal barb of the mating plug, a feature not present in other vaejovids) ... the presence of a spiny distal barb margin on the spermatophore mating plug is a potential synapomorphy uniting the *eusthenura*, *punctipalpi*, and *intrepidus* groups, *Syntropis*, and *Paravaejovis*.

Stockwell's (1992) observation was prescient, for the group of genera and species mentioned above, and the synapomorphy uniting them, corresponds to the monophyletic group of taxa recovered in the analyses of González-Santillán and Prendini (in press) and redefined as subfamily Syntropinae in the present contribution. In spite of observing that the distal barb margin is "armed with a row of teeth ... in the *V. punctipalpi* and *V. eusthenura* groups, *Syntropis*, and *Paravaejovis*," Stockwell (1989: 131, 132) followed Haradon's (1984b) opinion that *Paravaejovis* shares "many derived character states with *Paruroctonus*, *Smeringurus* and *Vejovoidus*," and grouped it with these genera in his unpublished tribe "Paruroctonini" (table 2).

Sissom (2000: 503) summarized the taxonomic history and generic and species composition of Vaejovidae, listing 10 genera and five species groups (the *eusthenura*, *intrepidus*, *mexicanus*, *nitidulus*, and *punctipalpi* groups) of the putatively paraphyletic genus *Vaejovis*, and noted that "the phylogenetic relationships of the genera are still obscure, and it is not possible at this time to recognize subfamilies or tribes ... [but] it is likely that such a classification will be a reality before long."

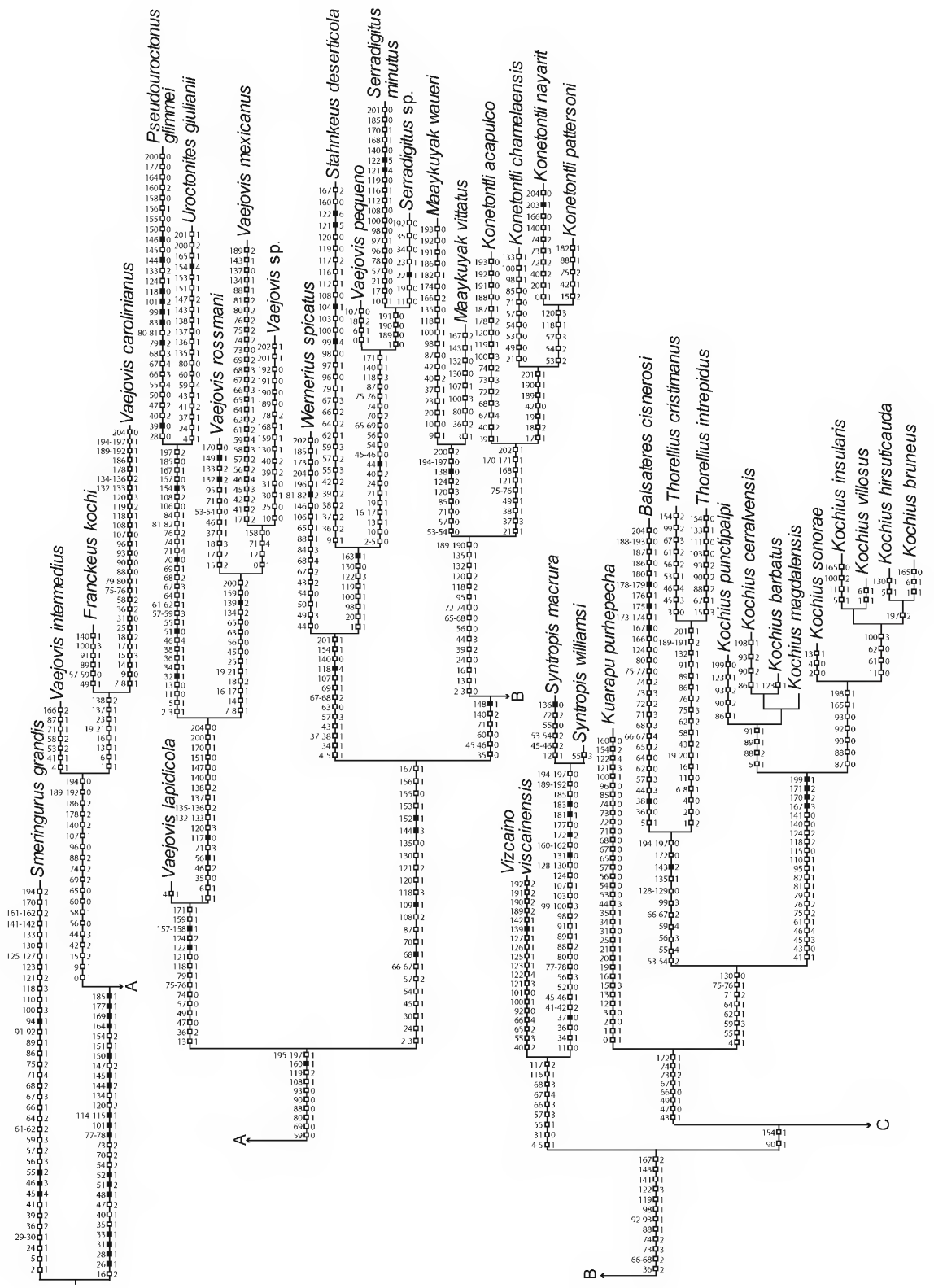
Two of Stockwell's (1989) generic names were subsequently published by Ponce-Saavedra and Beutelspacher (2001), without designating type species, and are therefore nomina nuda (table 2). Soleglad and Fet (2005, 2006, 2008) coopted the rest of Stockwell's (1989) unpublished revisions to the generic and suprageneric classification of the Vaejovidae with some, mostly nomenclatural variations (table 3). Syntropinae was restricted to Stockwell's (1989) former tribe "Syntropini." *Serradigitus* Stahnke, 1974 and three new genera were separated into tribe Stahnkeini Soleglad and Fet, 2006, from *Syntropis* and another three "new" genera, created to accommodate the former *eusthenura*, *intrepidus*, and *punctipalpi* groups of *Vaejovis*, which were placed in two subtribes of Syntropini. Stockwell's (1989) tribe "Paruroctonini" was removed from Syntropinae and renamed subfamily Smeringurinae Soleglad and Fet, 2008, with a monotypic tribe Paravaejovini Soleglad and Fet, 2008, erected for *Paravaejovis*. No quantitative cladistic analysis justifying these changes, many taken directly from Stockwell's (1989) unpublished dissertation (vide Soleglad and Fet 2008: 1, 2), was presented by these authors. Most of the "new" genera are names for species groups proposed by others (Hoffmann, 1931; Williams, 1970a, 1971a; Sissom and Francke, 1985; Sissom, 1989), the monophyly of which has never been tested, and the diagnoses of which rely heavily on morphometrics lacking any theoretical basis (e.g., "maximized ratios"; Fet and Soleglad, 2002: 5).

Kuarapu Francke and Ponce-Saavedra, 2010, another genus related to Syntropinae based on the spinose margin of the distal barb of the hemimating plug, was recently described. Francke and Ponce-Saavedra (2010) discussed its placement in the context of Soleglad and Fet's (2008) classification of Vaejovidae, noting that the classification was not rigorously assessed and that when it is evaluated, several components may prove not to be monophyletic. Their prediction has since been confirmed and yet another revised classification is in order.

MATERIAL AND METHODS

Scorpion specimens were collected mostly by ultraviolet (UV) light detection at night (Stahnke, 1972) using portable UV lamps, comprising mercury-vapor tubes attached to a chromium reflector, and powered by a 12V, 7 amp/hour battery, or Maglite flashlights modified with UV LED attachments. Some specimens were collected by turning rocks and other objects on the ground, during the day.

Material examined is deposited in the following collections: American Museum of Natural History, New York (AMNH); Colección de Aracnología y Entomología del Centro de Investigaciones Biológicas del Noroeste, Baja California Sur, Mexico (CAECIB); California Academy of Sciences, San Francisco, California (CAS); Colección Nacional de Arácnidos, Instituto de Biología,


Smeringurus grandis
Vaejovis intermedius
Franckeus kochi
Vaejovis carolinianus
Vaejovis lapidicola
Uroctonites giulianii
Pseudouroctonus glimmei
Vaejovis rossmani
Vaejovis mexicanus
Vaejovis sp.
Wernerius spicatus
Stahnkeus deserticola
Vaejovis pequeno
Serradigitus minutus
Serradigitus sp.
Maaykuyak waueri
Maaykuyak vittatus
Konetontli acapulco
Konetontli chamelaensis
Konetontli nayarit
Konetontli pattersoni
Syntropis macrura
Syntropis williamsi
Vizcaino viscainensis
Kuarapu purhepecha
Balsateres cisnerosi
Thorellius cristimanus
Thorellius intrepidus
Kochius punctipalpi
Kochius cerralvensis
Kochius barbatus
Kochius magdalensis
Kochius sonorae
Kochius insularis
Kochius villosus
Kochius hirsuticauda
Kochius bruneus
A
B
C

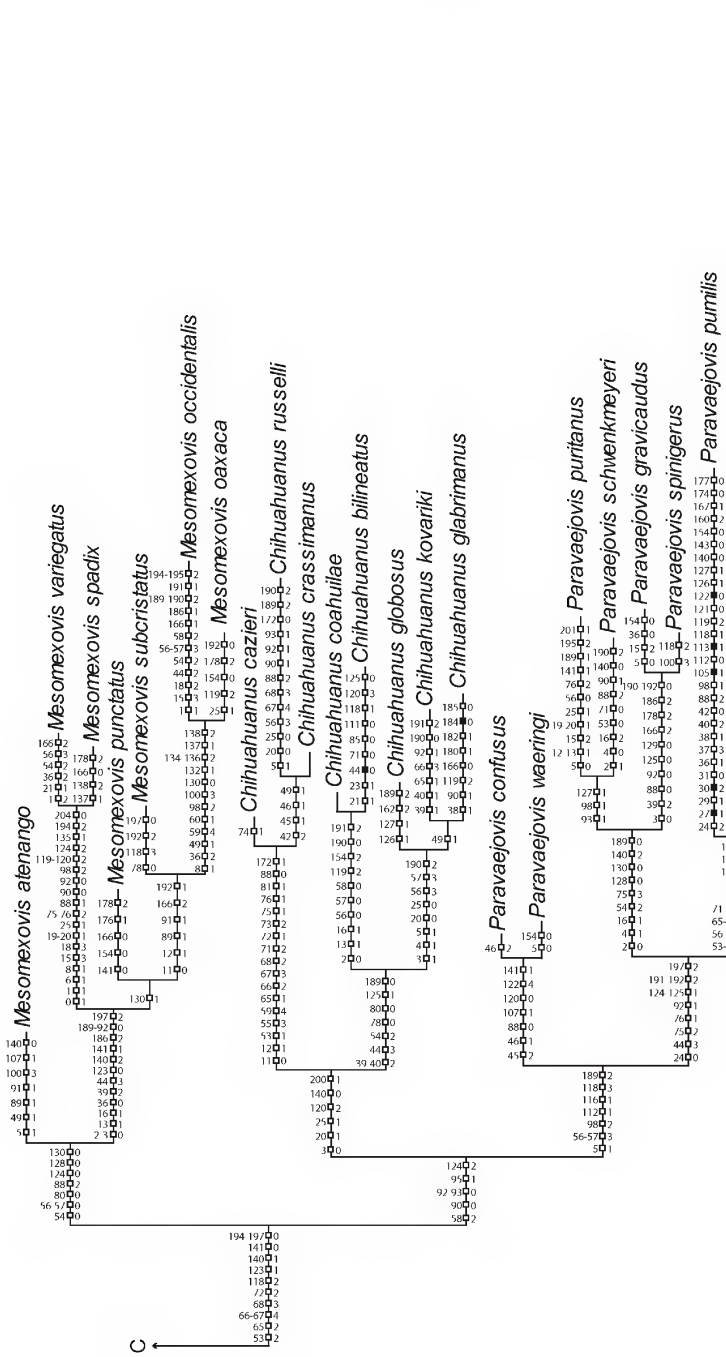


Fig. 7. Most parsimonious tree (length: 10894.593, CI: 0.190, RI: 0.628, fit: 244.08), obtained by simultaneous phylogenetic analysis of 250 qualitative and quantitative morphological characters and 4221 aligned DNA nucleotides from three mitochondrial and two nuclear gene markers, for 18 genera and 61 species in the North American vaejovid scorpion subfamily Syntropinae Kraepelin, 1905. Analyses were conducted with an implied weighting regime ($k = 18$) that maximized average support (González-Santillán and Prendini, in press). Synapomorphies are optimized with accelerated transformation. Black bars indicate uniquely derived apomorphic states, white bars indicate parallel derivations of apomorphic states, numbers above indicate characters, and numbers below indicate states (appendix 1).

TABLE 2
Unpublished generic and suprageneric classification of the North American scorpion family Vaejovidae Thorell, 1876, proposed by Stockwell (1989)

Syntropinae Kraepelin, 1905[1]
"Paruroctonini"
Paravaejovis Williams, 1980
Paruroctonus Werner, 1934
Smeringurus Haradon, 1983[1]
Vejovoidus Stahnke, 1974
"Sissomiini"
Sissomius Ponce-Saavedra and Beutelspacher, 2001, nomen nudum[2] [= *Vaejovis nitidulus* group]
Syntropini Kraepelin, 1905
"*Franckeus*" [= *Vaejovis punctipalpi* group]
Lissovaejovis Ponce-Saavedra and Beutelspacher, 2001, nomen nudum[2] [= *Vaejovis eusthenura* group]
Serradigitus Stahnke, 1974
Syntropis Kraepelin, 1900
"Uroctonini"
Pseudouroctonus Stahnke, 1974 [= *Vaejovis minimus* group, in part][1]
Uroctonites Williams and Savary, 1991
Uroctonus Thorell, 1876
Vaejovinae Thorell, 1876
Vaejovis C.L. Koch, 1836

[1]Stockwell (1992) synonymized Syntropinae with Vaejovidae, elevated *Smeringurus* to the rank of genus from its former rank as a subgenus of *Paruroctonus*, and revised the diagnosis of *Pseudouroctonus* to include the former *minimus* group of *Vaejovis*.

[2]Ponce-Saavedra and Beutelspacher (2001) published two of Stockwell's (1989) names, "*Lissovaejovis*" and "*Sissomius*," without designating type species for either.

[3]Stockwell (1989) applied the name "*Franckeus*" to the former *punctipalpi* group of *Vaejovis*. Soleglad and Fet (2005) published the name "*Franckeus*" but applied it to a subsection of the former *nitidulus* group of *Vaejovis*.

TABLE 3
Generic and suprageneric classification of the North American scorpion family Vaejovidae Thorell, 1876, proposed by Soleglad and Fet (2003, 2005, 2006, 2008)

Smeringurinae Soleglad and Fet, 2008
Paravaejovini Soleglad and Fet, 2008
Paravaejovis Williams, 1980
Smeringurini Soleglad and Fet, 2008
Paruroctonus Werner, 1934
Smeringurus Haradon, 1983
Vejovoidus Stahnke, 1974
Syntropinae Kraepelin, 1905
Stahnkeini Soleglad and Fet, 2006
Gertschius Graham and Soleglad, 2007
Serradigitus Stahnke, 1974
Stahnkeus Soleglad and Fet, 2006
Wernerius Soleglad and Fet, 2008
Syntropini Kraepelin, 1905
Syntropina Kraepelin, 1905
Hoffmannius Soleglad and Fet, 2008 [= *Vaejovis eusthenura* group]
Syntropis Kraepelin, 1900
Thorelliina Soleglad and Fet, 2008
Kochius Soleglad and Fet, 2008 [= *Vaejovis punctipalpi* group]
Thorellius Soleglad and Fet, 2008 [= *Vaejovis intrepidus* group]
Vaejovinae Thorell, 1876
Franckeus Soleglad and Fet, 2005[1] [= *Vaejovis nitidulus* group, in part]
Pseudouroctonus Stahnke, 1974
Uroctonites Williams and Savary, 1991
Vaejovis C.L. Koch, 1836

[1]Stockwell (1989) applied the name "*Franckeus*" to the former *punctipalpi* group of *Vaejovis*. Soleglad and Fet (2005) published the name "*Franckeus*" but applied it to a subsection of the former *nitidulus* group of *Vaejovis*.

Universidad Nacional Autónoma de México, Mexico City (IBUNAM); Muséum d'Histoire Naturelle de Genéve, Switzerland (MHNG); Ohio State University, Museum of Biological Diversity, Columbus, Ohio (OSAL). Specimens at the AMNH, CAS and IBUNAM bearing ARA (Arachnida) numbers were collected during a U.S. National Science Foundation–funded "Revisionary Syntheses in Systematics" grant.

Measurements (mm) were taken with an ocular micrometer and illustrations of external morphology produced using a Nikon SMZ 1500 stereomicroscope with a camera lucida. Photomicrographs were taken under visible and UV light using a Microptics ML-1000 digital imaging system.

Morphological terminology follows Vachon (1974) for trichobothria, Sissom (1991) for hemispermatophore (fig. 8), and Stahnke (1970) for other characters, except as noted. The terms "internal" and "external" are replaced with "prolateral" and "retrolateral," following Acosta et al. (2008). Pedipalp carination (figs. 9–11) follows a system developed by Prendini et al. (in prep.). The pedipalp chela finger dentition of Soleglad and Sissom (2001) is redefined to maintain consistency with the terminology for pedipalp

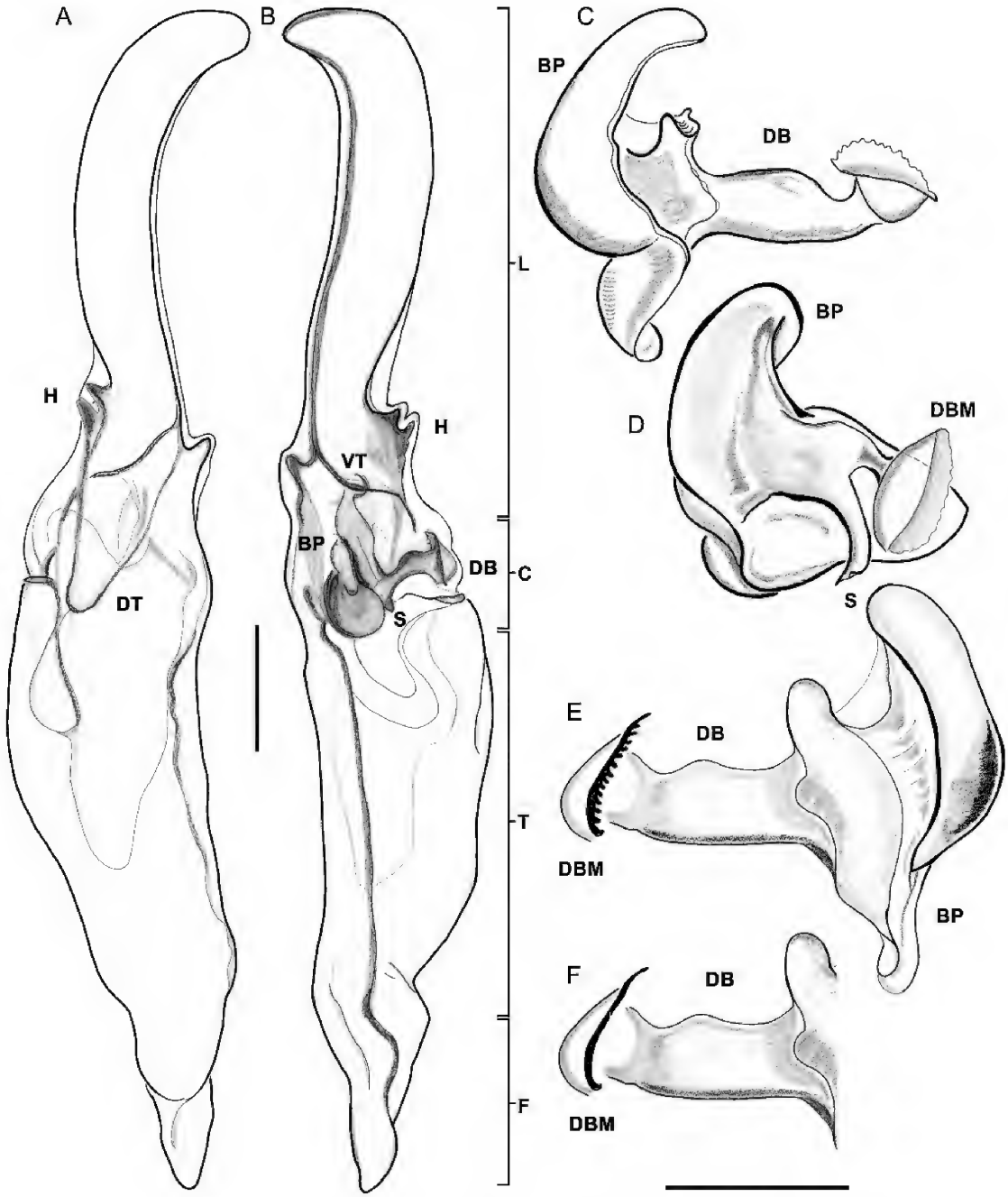


Fig. 8. *Syntropis williamsi* Soleglad et al., 2007, ♂ (AMNH), (**A–E**) and *Stahnkeus deserticola* (Williams, 1970), ♂ (AMNH), (**F**), dextral hemispermatophore (**A, B**) and microstructures of hemimating plug (**C–F**). **A, E, F.** Dorsal aspect. **B, C.** Ventral aspect. **D.** Ental aspect. Abbreviations: **BP,** basal plate; **C,** capsule; **F,** foot; **H,** laminar hook; **L,** lamina; **DB,** distal barb; **DBM,** distal barb margin; **DT,** dorsal trough; **S,** spine; **T,** trunk; **VT,** ventral trough. Scale bars = 1 mm (**A, B**), 0.5 mm (**C–F**).

segments (fig. 12). Leg setation and spinules (figs. 13, 14) are modified from McWest (2009). Metasomal carination (fig. 15) is modified from Ochoa et al. (2010).

Localities were georeferenced in the field with a portable GPS (Garmin® II Plus) or retroactively using GEOLocate (Rios and Bart, 2010) and Google Earth version 6.1.0.5001. Distribution maps were generated using ArcMap 9.3.1 (Environmental Systems Research Institute, Redlands, California), by superimposing point locality records on layers depicting the topography of North America, generated from digital elevation model files with 1 arc degree of resolution, obtained from the United States Geological Survey.

SYSTEMATICS

Family Vaejovidae Thorell, 1876
Subfamily Syntropinae Kraepelin, 1905

Syntropinae Kraepelin, 1905: 340, type genus *Syntropis* Kraepelin, 1900; Birula, 1917a: 163, 1917b: 57; Werner, 1934: 281; Mello-Leitão, 1945: 118; Millot and Vachon, 1949: 428; Brues et al., 1954: 704; Gertsch, 1958: 14, 15; Stahnke, 1974: 112, 113; Stockwell, 1992: 408; Sissom, 2000: 107; Soleglad and Fet, 2003: 109; 2008: 1, 2, 4–6, 13, 26–28, 33, 35–40, 45, 46, 50, 51, 53, 54, 62, 69, 72–74, 76, 77, 82, 84–86, 88–90, 93–97, 103, figs. 34–36, 41–56, 122–125, 164–167, 183, 196, 202–204, tables 1–3, 8, 9.

Paravaejovini Soleglad and Fet, 2008, syn. nov.: 1, 3, 13, 36, 46, 51, 75, 82, 84, 102, figs. 57, 126, 196, 197, tables 2, 8, 9.

Syntropini: Soleglad and Fet, 2008: 1, 2, 4, 13, 30, 33, 34, 38, 40, 43, 45, 46, 49, 50, 51, 53, 54, 57, 69, 71–74, 76, 77, 84, 85, 89, 91, 94, 95, 103, figs. 75–82, 103–110, 122–124, 170–181, 194–196, 203, 204; tables 2, 3, 8, 9.

Syntropina: Soleglad and Fet, 2008: 1, 32, 46, 51, 53, 74, 76, 77, 90, 91, figs. 196, 203, table 9.

Thorelliina Soleglad and Fet, 2008, syn. nov.: 1, 45, 51, 53, 71, 74, 89, 91, 92, 95, 96, 103, figs. 196, 204, table 9.

DIAGNOSIS: The monophyletic group of vaejovid scorpion taxa redefined here as subfamily Syntropinae may be separated from all other vaejovid taxa by the following unique synapomorphy: margin of distal barb of sclerotized hemimating plug on hemispermatophore spinose (armed with spines, hooks or teeth; fig. 8C–E). The following other vaejovid taxa possess a sclerotized hemimating plug on the hemispermatophore, but the margin of the distal barb is smooth (i.e. not spinose; fig. 8F): the monophyletic group comprising *Gertschius* Graham and Soleglad, 2007, *Serradigitus*, *Stahnkeus* Soleglad and Fet, 2006, and *Wernerius* Soleglad and Fet, 2008, formerly included in Syntropinae as tribe Stahnkeini (Soleglad and Fet, 2008); *Franckeus* Soleglad and Fet, 2005, and the *nigrescens* group of *Vaejovis*; some species of the *mexicanus* group of *Vaejovis*, e.g., *Vaejovis vorhiesi* Stahnke, 1940; and some species of *Pseudouroctonus*, e.g., *Pseudouroctonus apacheanus* (Gertsch and Soleglad, 1972).

Syntropinae are most closely related to the monophyletic group comprising *Gertschius*, *Serradigitus*, *Stahnkeus*, and *Wernerius*, based on the fused sclerites of the female genital operculum, which are connected the entire length. Syntropinae may be further separated from these taxa as follows. The first to third pectinal teeth are unmodified in Syntropinae, but enlarged, ovoid, and devoid of sensilla in *Gertschius*, *Serradigitus*, *Stahnkeus*, and *Wernerius*. The pedipalp chela fingers of Syntropinae possess low, subserrated rows of denticles and small to moderately developed terminal retrolateral denticles (figs. 17–19), compared with the fingers of *Serradigitus* and *Stahnkeus*, which possess strongly serrated denticle rows and enlarged, hooklike denticles. Pedipalp chela trichobothrium *est* is situated between RD4 and RD5 (and/or associated macrosetae) in Syntropinae (figs. 10B, 17B, D, 18B, 19B, D) but between RD3 and RD4 (and/or associated macrosetae) in *Stahnkeus*. One to six pairs of ventrodistal spinules are present on the telotarsi of Syntropinae (figs. 21A–C, 22A, B), compared with only one pair on the telotarsi of *Gertschius*, *Serradigitus*, *Stahnkeus*, and *Wernerius*.

Additional diagnostic characters of Syntropinae are as follows: carapace with superciliary carinae usually higher than median ocelli (fig. 16); cheliceral serrula comprising up to 30 tines; pedipalp chela trichobothrium *Db* situated on or dorsal to the drl carina (figs. 10A, 17A, C, 18A, D, 19A, C); chela dps, plm, pld, and plvs carinae obsolete to costate, except in *Kochius* and a few species of *Chihuahuanus*, gen. nov., and *Thorellius* (figs. 10A, 11A, B, 17A, C, 18A); patella rlm

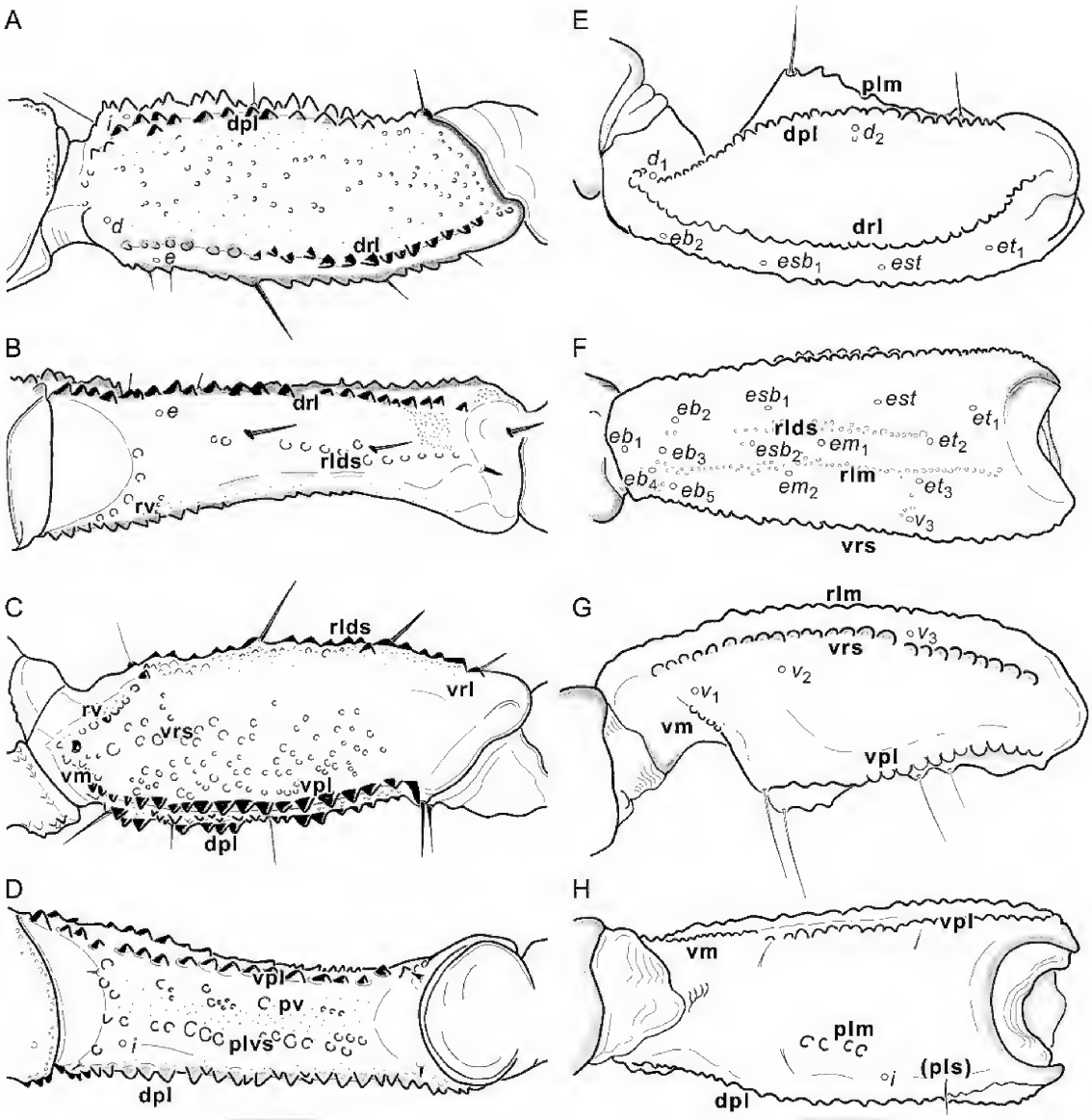


Fig. 9. *Kochius punctipalpi* (Wood, 1863), ♂ (AMNH), dextral pedipalp femur (**A–D**) and patella (**E–H**), dorsal (**A, E**), retrolateral (**B, F**), ventral (**C, G**) and prolateral (**D, H**) aspects, illustrating carinae (boldface) and trichobothria (italics). Abbreviations: **dpl,** dorsal prolateral; **drl**, dorsal retrolateral; **plm**, prolateral median; **pls,** prolateral subdorsal (absent in Syntropinae Kraepelin, 1905, but present in other vaejovids); **pv**, prolateral ventral; **plvs**, prolateral ventrosubmedian; **rlds**, retrolateral dorsosubmedian; **rv**, retrolateral ventral; **vm**, ventral median; **vpl**, ventral prolateral; **vrl**, ventral retrolateral; **vrs**, ventral retrosubmedian. *d*, dorsal; *e*, external; *eb*, external basal; *esb*, external suprabasal; *em*, external medial; *est*, external subterminal; *et*, external terminal; *i*, internal; *v*, ventral. Scale bars = 1 mm.

and rlds carinae obsolete to costate, except in *Kochius*, *Syntropis*, and a few species of *Thorellius* (fig. 9F); telotarsi I–IV each with two proventral setae, two or three retroventral macrosetae, and 1–6 pairs of ventrodistal spinules (figs. 13B, 21A–C, 22A, B); aculeus with lateral microserration vestigial to well developed.

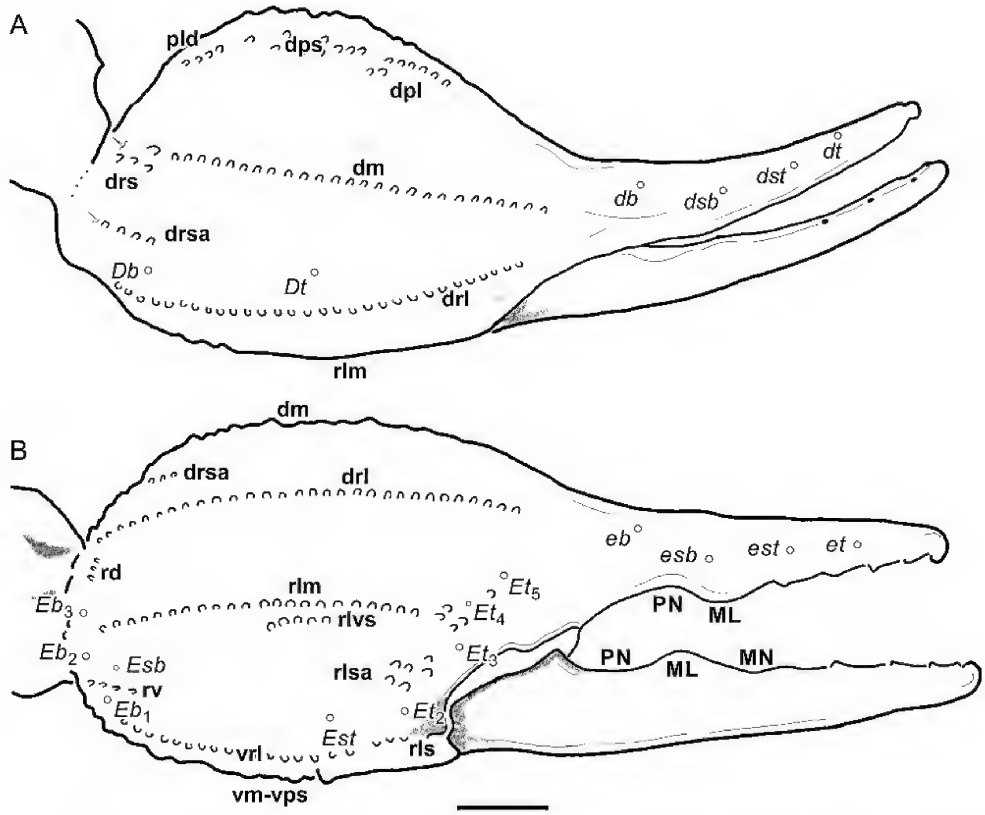


Fig. 10. *Kochius punctipalpi* (Wood, 1863), ♂ (AMNH), dextral pedipalp chela, dorsal (**A**) and retrolateral (**B**) aspects, illustrating carinae (boldface), finger lobes and notches (uppercase), and trichobothria (italics). Abbreviations: **dm**, dorsal median; **dpl**, dorsal prolateral; **dps**, dorsal prosubmedian; **drl**, dorsal retrolateral; **drs**, dorsal retrosubmedian; **drsa**, retrosubmedian accessory; **pld**, prolateral dorsal; **rd**, retrolateral dorsal; **rlm**, retrolateral median; **rls**, retrolateral subventral; **rlsa**, retrolateral subventral accessory; **rlvs**, retrolateral ventrosubmedian; **vm**, ventral median; **vps**, ventral prosubmedian; **vrl**, ventral retrolateral. **ML**, medial lobe; **MN**, medial notch; **PN**, proximal [= basal] notch. *db*, *Db* dorsal basal; *dsb*, dorsal suprabasal; *dst*, dorsal subterminal; *dt*, *Dt*, dorsal terminal; *eb*, *Eb*, external basal; *esb*, *Esb*, external suprabasal; *est*, *Est*, external subterminal; *et*, *Et*, external terminal. Scale bar = 1 mm.

INCLUDED GENERA: *Balsateres*, gen. nov.; *Chihuahuanus*, gen. nov.; *Kochius* Soleglad and Fet, 2008; *Konetontli*, gen. nov.; *Kuarapu* Francke and Ponce-Saavedra, 2010; *Maaykuyak*, gen. nov.; *Mesomexovis*, gen. nov.; *Paravaejovis* Williams, 1980; *Syntropis* Kraepelin, 1900; *Thorellius* Soleglad and Fet, 2008; *Vizcaino*, gen. nov.

DISTRIBUTION: Subfamily Syntropinae is endemic to Mexico and the United States (figs. 3–6). Species of the subfamily have been recorded from 27 states in Mexico (Aguascalientes, Baja California, Baja California Sur, Coahuila, Colima, Chiapas, Chihuahua, Durango, Estado de México, Guanajuato, Guerrero, Hidalgo, Jalisco, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Queretaro, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Tlaxcala, Veracruz, Zacatecas) and seven states in the United States (Arizona, California, Nevada, New Mexico, Oregon, Texas, Utah).

REMARKS: Based on phylogenetic analyses presented elsewhere (fig. 7; González-Santillán and Prendini, in press), Syntropinae is hereby restricted to the 11 genera listed above. Four genera, formerly accommodated in tribe Stahnkeini Soleglad and Fet, 2008, are hereby removed from Syntropinae: *Gertschius* Graham and Soleglad, 2007; *Serradigitus*

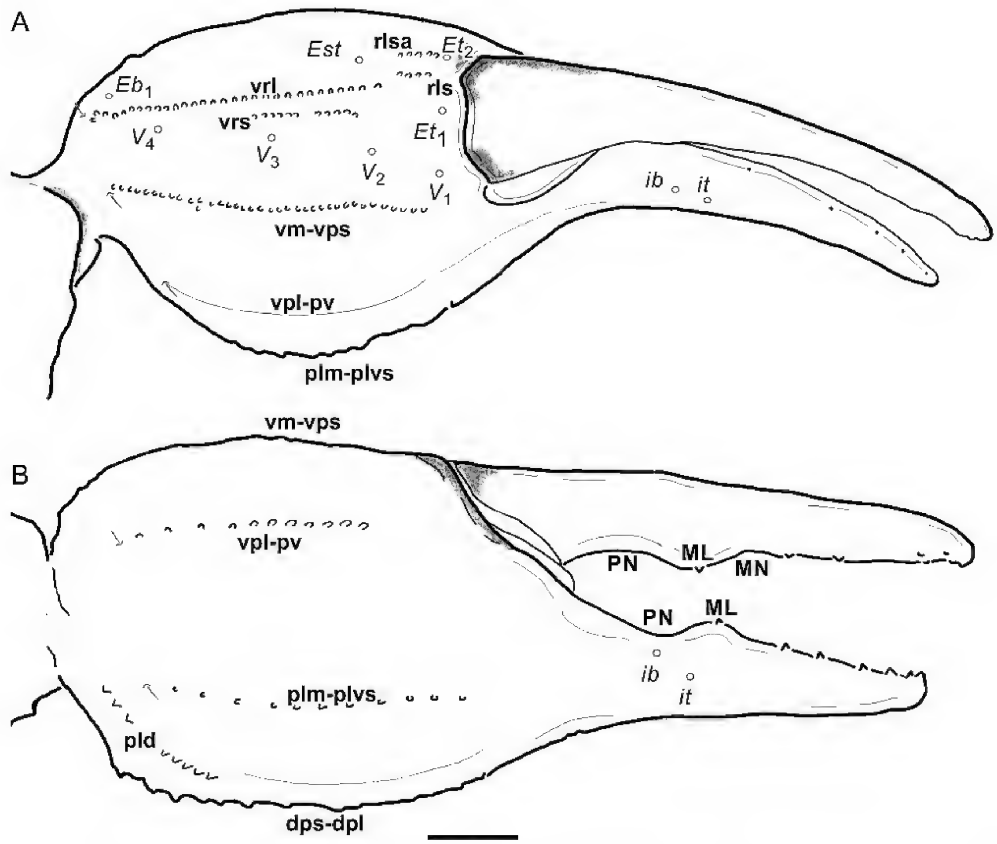


Fig. 11. *Kochius punctipalpi* (Wood, 1863), ♂ (AMNH), dextral pedipalp chela, ventral (**A**) and prolateral (**B**) aspects, illustrating carinae (boldface), finger lobes and notches (uppercase), and trichobothria (italics). Abbreviations: **dpl**, dorsal prolateral; **dps**, dorsal prosubmedian; **pld**, prolateral dorsal; **plm**, prolateral median; **pv**, prolateral ventral; **plvs**, prolateral ventrosubmedian; **rls**, retrolateral subventral; **rlsa**, retrolateral subventral accessory; **vm**, ventral median; **vpl**, ventral prolateral; **vps**, ventral prosubmedian; **vrl**, ventral retrolateral; **vrs**, ventral retrosubmedian. **ML**, medial lobe; **MN**, medial notch; **PN**, proximal [= basal] notch. *Eb*, external basal; *Est*, external subterminal; *Et*, external terminal; *ib*, internal basal; *it*, internal terminal; *V*, ventral. Scale bar = 1 mm.

Stahnke, 1974; *Stahnkeus* Soleglad and Fet, 2006; *Wernerius* Soleglad and Fet, 2008.

KEY TO IDENTIFICATION OF THE GENERA OF SYNTROPINAE

1. Telson, dorsal surface (adult ♂, ♀) with whitish glandular area (fig. 26); metasomal segment V, ventral surface glabrous (smooth) to matte; pedipalp chela fixed finger, median denticle row with five primary subrows of median denticles and five prolateral denticles 2
– Telson, dorsal surface (adult ♂, ♀) without whitish glandular area; metasomal segment V, ventral surface matte to shagreened; pedipalp chela fixed finger, median denticle row with five or six primary subrows of median denticles and five or six prolateral denticles 3
2. Telson, dorsal surface (adult ♂, ♀) with small fusiform, whitish glandular area anterior to base of aculeus (fig. 26A; may be minute in *Chihuahuanus bilineatus* (Pocock, 1898), comb. nov.); pedipalp chela, fixed finger trichobothrium *et* situated midway between RD3 and RD4 or closer to RD3 than to RD4 (fig. 17B) . . . . . *Chihuahuanus*, gen. nov.
– Telson, dorsal surface (adult ♂, ♀) with medium-sized oval, whitish glandular area medially (fig. 26B; may be reduced in adult ♀); pedipalp chela, fixed finger trichobothrium *et* aligned with or closer to RD4 than to RD3 . . . . . *Maaykuyak*, gen. nov.

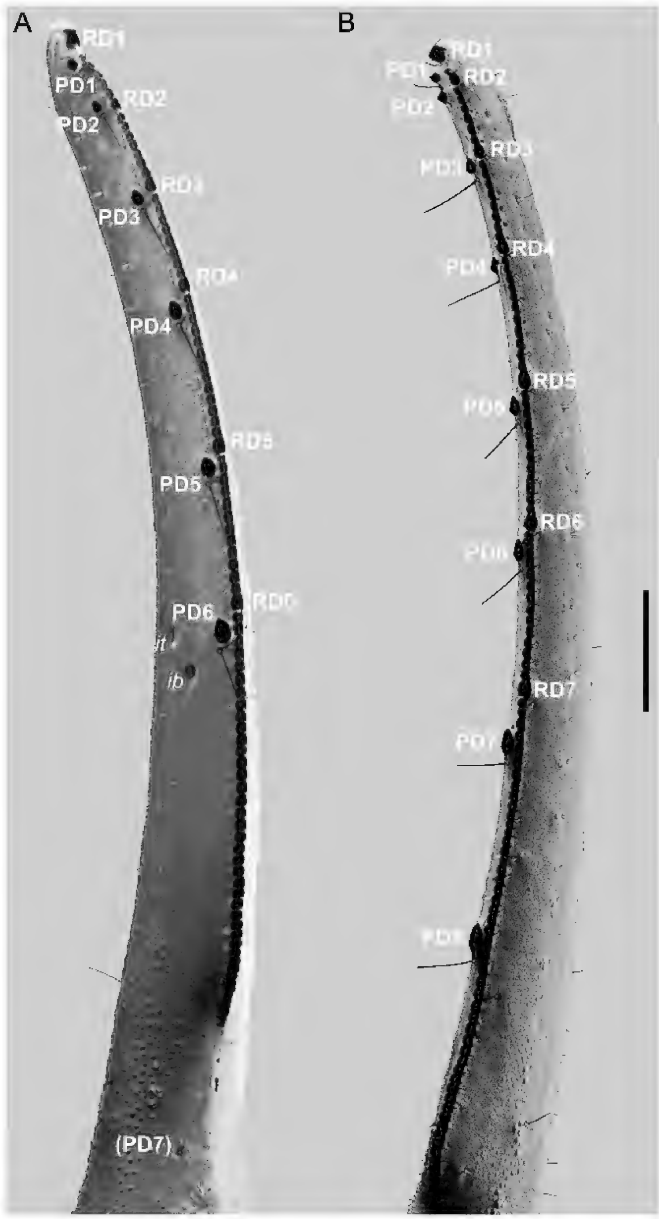


Fig. 12. *Syntropis williamsi* Soleglad et al., 2007, ♂ (AMNH), dextral pedipalp fixed (**A**) and movable (**B**) fingers, ventral and dorsal aspect respectively, illustrating denticles and/or associated macrosetae (uppercase), and trichobothria (italics). Abbreviations: **PD**, prolateral denticle; **RD**, retrolateral denticle and/or associated macroseta. *ib*, internal basal; *it*, internal terminal. Scale bar = 1 mm.

3. Sternite VII, ventral surface (adult ♂, ♀) with whitish glandular area medially (fig. 23). . . 4
– Sternite VII, ventral surface (adult ♂, ♀) without whitish glandular area 6
4. Sternite VII, ventral surface (adult ♂, ♀) with whitish glandular area between ventrosubmedian carinae, extending almost entire length of segment (fig. 23B); metasomal segments I–IV, ventrosubmedian carinae absent, ventromedian carinae present, smooth to finely granular (fig. 24C). . . . . *Syntropis*
– Sternite VII, ventral surface (adult ♂, ♀) with raised, whitish triangular boss, restricted to posteromedial third of segment; metasomal

segments I–IV, ventrosubmedian carinae present, granular, ventromedian carinae absent (fig. 24A, B). 5

5. Pedipalp chela manus (adult ♂, ♀) incrassate, with carinae well developed, granular and immaculate (fig. 18A, B); sternite VII, ventrolateral surfaces shagreened; telson (♀), lateral and especially ventral surfaces, macrosetae as long as or longer than aculeus (fig. 25A) . . . . *Kochius*
– Pedipalp chela manus (adult ♂, ♀) slender, with carinae obsolete and infuscate (fig. 18C, D); sternite VII, ventrolateral surfaces glabrous; telson (♀), lateral and ventral surfaces, macrosetae shorter than aculeus. . . . *Kuarapu*
6. Pedipalp chela movable finger, median denticle row with five retrolateral denticles and four primary subrows of median denticles, terminal row absent (fig. 20C); legs I–III, basitarsi, dorsal and retrodorsal macrosetae elongated, arranged into sublinear row, forming setal comb (fig. 21C); telotarsi, ventral spinules elongate and slender (fig. 21C). . . . . *Vizcaino*, gen. nov.
– Pedipalp chela movable finger, median denticle row with five or more retrolateral denticles and more than four primary subrows of median denticles, terminal row present (figs. 12B, 17C, 19A, C, 20A, B); legs I–III, basitarsi, dorsal and retrodorsal macrosetae usually short and arranged into separate rows, not forming setal comb (fig. 21B), except in *Paravaejovis pumilis* (Williams, 1980) (fig. 22C); telotarsi, ventral spinules short and stout (fig. 21B). 7
7. Total body length (adult ♂, ♀) less than 25 mm; telotarsi each with one pair of ventrodistal spinules; telson with conspicuous subaculear tubercle (figs. 25B, C, 28B) . . . . . *Konetontli*, gen. nov.
– Total body length (adult ♂, ♀) more than 26 mm; telotarsi each with two or more pairs of ventrodistal spinules (fig. 21B; except in *P. pumilis*, fig. 22C); telson without conspicuous subaculear tubercle (figs. 27B, C, 28A, C) . . . 8
8. Carapace and tergites densely infuscate, except in *Mesomexovis atenango* (Francke and González-Santillán, 2007), comb. nov.; pedipalp chela manus, dorsal carinae (dm, dpl, drl, drs, drsa) smooth (fig. 19A, B); metasomal segments I–IV, ventrosubmedian and ventrolateral carinae infuscate, ventrosubmedian carinae absent on I and II, obsolete to weakly granular on III and IV (fig. 27B) . . . . . *Mesomexovis*, gen. nov.
– Carapace and tergites immaculate to weakly infuscate; pedipalp chela manus, dorsal carinae (dm, dpl, drl, drs, drsa) smooth or granular (figs. 17C, D, 19C, D); metasomal segments I–IV, ventrosubmedian and ventrolateral carinae immaculate to weakly infuscate, ventrosubmedian carinae absent to obsolete on I and II, weakly costate to strongly granular on III and IV (fig. 27C) 9
9. Habitus gracile, total body length (adult ♂, ♀) 37–68 mm; base color pale, yellowish (fig. 1C); pedipalp chela manus, carinae obsolete to weakly developed, barely protruding above intercarinal surfaces, and rarely granular; trichobothrium Et_5 situated at base of fixed finger far removed from trichobothrium Et_4 (fig. 19D), less obvious in *P. pumilis* . . . . . *Paravaejovis*
– Habitus robust, total body length (adult ♂, ♀) 45–94 mm; base color dark brown to reddish, except in *Balsateres cisnerosi* (Ponce-Saavedra and Sissom, 2004), comb. nov.; pedipalp chela manus, carinae well developed, protruding markedly above intercarinal surfaces, smooth or granular (fig. 17C, D); trichobothrium Et_5 situated on manus close to trichobothrium Et_4 (fig. 17C, D) 10
10. Carapace, pedipalp chela and patella, tergites, metasoma, and telson, carinae and intercarinal surfaces smooth (figs. 16A, 28A); base color pale, yellowish; tergites immaculate; metasomal macrosetae counts low: dl, 0/0:0/0:0/0:1/1:4/4; lm, 0/0:0/0:0/0:0/0:2/2; vl and vsm, 1/1:1/1:1/1:1/1:3/3; pedipalp chela fingers, proximal gap weak to obsolete . . . . . *Balsateres*, gen. nov.
– Carapace, pedipalp chela and patella, tergites, metasoma, and telson, carinae and intercarinal surfaces granular or crenulate (figs. 17C, D); base color dark brown to reddish; tergites infuscate; metasomal macrosetae counts moderate: dl, 2/2:3/3:3/3:3/3:7/6; lm, 1/1:3/3:3/3:4/4:4/4; vl, 2/2:3/3:3/3:3/3:7/7; vsm, 3/3:3/3:3/3:3/3:5/5 or greater; pedipalp chela fingers, proximal gap moderate to strong . . . . *Thorellius*

Balsateres, gen. nov.

Figures 3, 7, 16A, 20A, 28A; table 1

Vaejovis cisnerosi Ponce-Saavedra and Sissom, 2004 [= *Balsateres cisnerosi* (Ponce-Saavedra and Sissom, 2004), comb. nov.], type species, by monotypy.

Thorellius (part): Soleglad and Fet, 2008: 1, 95, 102; Ayrey and Soleglad, 2011: 1.

Vaejovis intrepidus group (part): Santibáñez-López and Sissom, 2010: 52.

ETYMOLOGY: The name *Balsateres*, gen. nov., a compound word, masculine in gender, is derived from the Balsas Depression, to

Fig. 13. *Syntropis williamsi* Soleglad et al., 2007, ♂ (AMNH), dextral leg II, basitarsus and telotarsus, dorsal (**A**) and ventral (**B**) aspects, illustrating rows of spinules. Abbreviations: **pv**, prolateral ventral; **rd**, retrolateral dorsal; **rl**, retrolateral; **rv**, retrolateral ventral; **vd**, ventral distal; **vm**, ventral median. Scale bar = 1 mm.

Fig. 14. *Syntropis williamsi* Soleglad et al., 2007, ♂ (AMNH), dextral leg II, basitarsus and telotarsus, dorsal (**A**) and ventral (**B**) aspects, illustrating distribution of macrosetae. Abbreviations: **D**, dorsal; **PD**, prolateral dorsal; **PM**, prolateral median; **PV**, prolateral ventral; **RD**, retrolateral dorsal; **RM**, retrolateral median; **RV**, retrolateral ventral. Scale bar = 1 mm.

which the genus is endemic, and the Latin adjective *teres* ("smooth" or "polished") which refers to the glabrous integument typical of this genus.

DIAGNOSIS: *Balsateres*, gen. nov., is distinguished from other genera of Syntropinae by the smooth dl carinae on metasomal segments I–IV. The carinae and intercarinal surfaces of the carapace (fig. 16A), pedipalp chela, patella, tergites, metasoma, and telson (fig. 28A) are smooth in this genus. Counts of macrosetae on the carinae of metasomal segments I–IV are also greatly reduced, as follows: dl, 0/0:0/0:0/0:1/1:4/4; lm, 0/0:0/0:0/0:0/0:2/2; vl and vsm, 1/1:1/1:1/1:1/1:3/3. Two or more macrosetae are present on these carinae in all other Syntropinae, including *Thorellius*, which also presents low setal counts, e.g., *Thorellius cristimanus* (Pocock, 1989) with the following counts on segments I–V: dl, 2/2:3/3:3/3:3/3:7/6; lm, 1/1:3/3:3/3:4/4:4/4; vl, 2/2:3/3:3/3:3/3:7/7; vsm, 3/3:3/3:3/3:3/3:5/5.

Balsateres, gen. nov., is most closely related to *Thorellius* (fig. 7), with which it shares broad pedipalpal and metasomal carinae and, with *Thorellius intrepidus* (Thorell, 1867), double basal prolateral denticles on the movable finger of the pedipalp chela (fig. 20A, B). However, all carinae are smooth in *Balsateres*, gen. nov., instead of moderately to densely granular, as in *Thorellius*. The distinct proximal gap, evident when the pedipalp chela fingers are closed, in both sexes of *Thorellius*, is absent in *Balsateres*, gen. nov. The two genera also differ in base coloration and infuscation. *Balsateres*, gen. nov., is yellowish and almost immaculate, except for the ocular tubercle, which is outlined by dark infuscation, whereas *Thorellius* tend to be darker and reddish in color, with various degrees of infuscation on the carapace and tergites.

Balsateres, gen. nov., resembles *Mesomexovis*, gen. nov., in possessing obsolete ventral carinae on metasomal segments I–IV, but species of the latter genus differ in being more setose and infuscate.

INCLUDED SPECIES: *Balsateres cisnerosi* (Ponce-Saavedra and Sissom, 2004), comb. nov.

DISTRIBUTION: *Balsateres*, gen. nov., is endemic to the Balsas Depression of Mexico and recorded only from Estado de México and Michoacán (fig. 3).

NATURAL HISTORY: *Balsateres*, gen. nov., inhabits tropical deciduous forest at altitudes between 195–672 m. Specimens were observed at night, doorkeeping at the entrances of their burrows in open, sandy areas, and excavated from the burrows (Ponce-Saavedra and Sissom, 2004). The glabrous integument and burrowing biology in sandy habitats suggest that this species is psammophilous although the leg setation is atypical for the psammophilous ecomorphotype, because the dorsal and retrolateral dorsal macrosetae are arranged into two separate rows, not forming a setal comb. This monotypic genus was collected at the same locality as another monotypic syntropine genus, *Kuarapu*. Although sympatric, these genera are allotopic: *Balsateres*, gen. nov., was collected in open, sandy areas, whereas *Kuarapu* was collected on road-cuts, suggesting a lithophilous ecomorphotype.

REMARKS: Due to the unique morphology of this species, Ponce-Saavedra and Sissom (2004) refrained from assigning it to one of the five species groups of *Vaejovis* recognized at the time. Soleglad and Fet (2008) transferred it to *Thorellius*, a name devised for Hoffmann's (1931) "second section" of *Vaejovis*, later termed the *intrepidus* group by Sissom (1989), without quantitatively testing its monophyly or composition. Santibáñez-López and Sissom (2010) also referred this species to the *intrepidus* group. The creation of a monotypic genus is merited by the unique diagnostic character combination of this species.

MATERIAL EXAMINED: *Balsateres cisnerosi* (Ponce-Saavedra and Sissom, 2004), comb. nov.: **MEXICO: Michoacán:** *Municipio de La Huacana*: El Vado, 18°48.908′N 101°54.976′W, 198 m, 20.v.2007, O.F. Francke, J. Ponce, M. Villaseñor, and A. Quijano, 1♂, 1♀ (IBUNAM).

Chihuahuanus, gen. nov.

Figures 1A, 2A, 4, 7, 16B, 17A, B, 21A, 26A, 27A; table 1

Vaejovis bilineatus Pocock, 1898 [= *Chihuahuanus bilineatus* (Pocock, 1898), comb. nov.], type species, here designated.

Vejovis first section (part): Hoffmann, 1931: 134, 139.

Vejovis spinigerus group (part): Williams, 1968: 16; 1970d: 238.

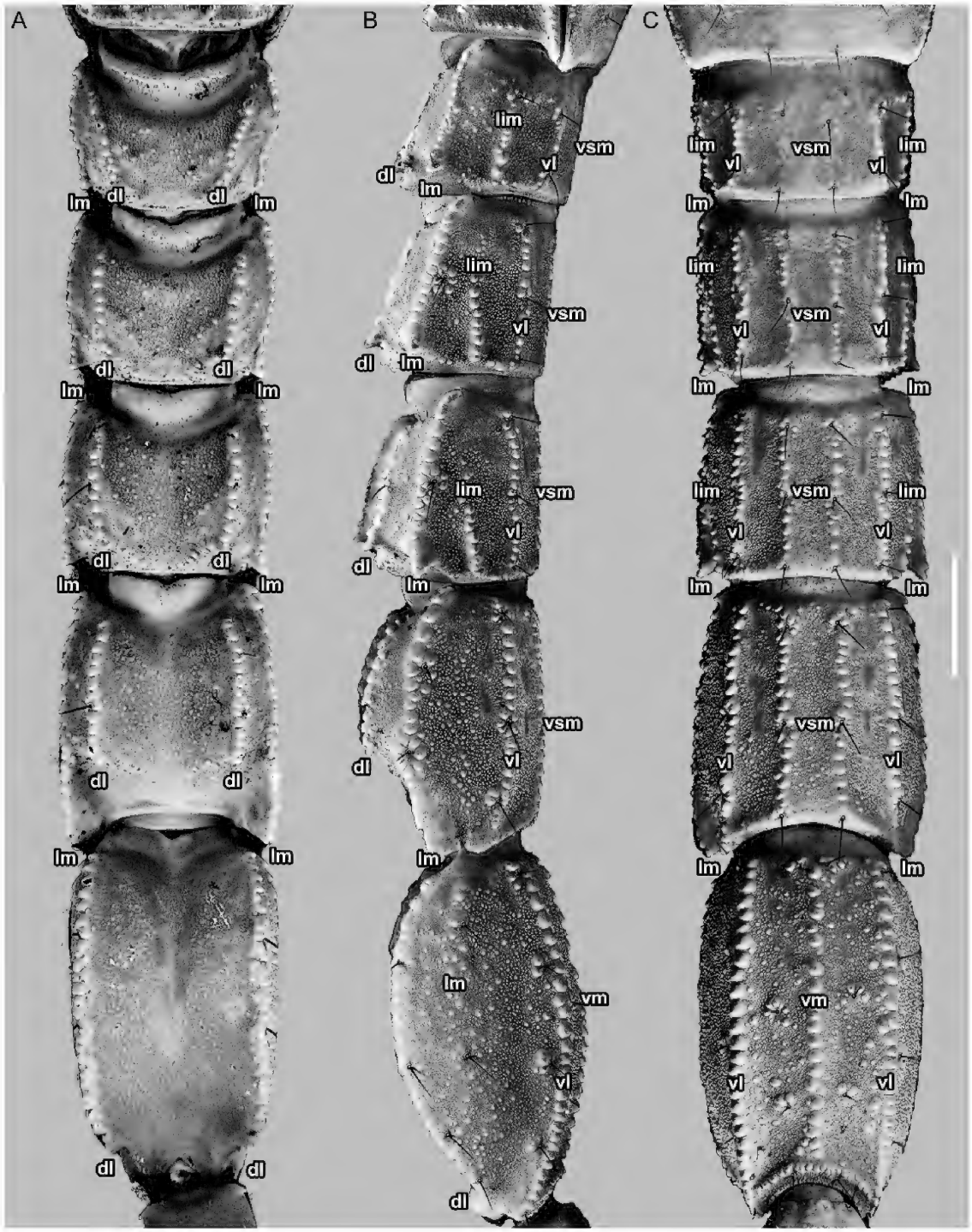


Fig. 15. *Konetontli pattersoni* (Williams and Haradon in Williams, 1980), comb. nov., ♂ (IBUNAM), metasomal segments I–V, dorsal (**A**), lateral (**B**) and ventral (**C**) aspects, illustrating carinae. Abbreviations: **dl**, dorsal lateral; **lim**, lateral inframedian; **lm**, lateral median; **vl**, ventral lateral; **vm**, ventral median; **vsm**, ventral submedian. Scale bar = 1 mm.

Vejovis eusthenura group (part): Williams, 1970a: 395, 396

Vejovis punctipalpi group (part): Williams, 1971a: 44–47; figs. 1, 2; table 1.

Vaejovis eusthenura group (part): Williams, 1980: 55; Sissom and Francke, 1985: 1; Sissom, 1991: 26; Stockwell, 1992: 408, 409; Sissom, 1993: 68; Yahia and Sissom, 1996: 86; Lourenço and Sissom, 2000: 135; Sissom, 2000: 530, 532, 551; Armas and Martín-Frías, 2001: 8; McWest, 2009: 8, 48, 52, 56, 61, 64, 98, 101–103, 108, table 1; Ponce-Saavedra and Sissom, 2004: 541; González-Santillán, 2004: 29; Francke and Ponce-Saavedra, 2005: 67; Sissom and Hendrixson, 2005a: 131; 2005b: 33, 34; Graham and Fet, 2006: 8, 9; Fet et al., 2006a: 9, table 1; 2006b: 8; 2006c: 7; Graham and Soleglad, 2007: 9, 11, 12; Soleglad et al., 2007: 134, 135; Santibáñez-López and Sissom, 2010: 49.

Vaejovis punctipalpi group (part): Williams, 1971a: 37; 1971b: 44; 1980: 80; Sissom and Francke 1985: 1; Sissom, 1989: 180; 1991: 26; Stockwell, 1992: 408, 409; Sissom, 1993: 68; Lourenço and Sissom, 2000: 135; Sissom, 2000: 548, 549, 551; Armas and Martín-Frías, 2001: 1; Hendrixson, 2001: 1; McWest, 2009: figs. 322–326, tables 1, 53, 89, 91, 93, 101–105, 108, 123; Ponce-Saavedra and Sissom, 2004: 539, 541; Sissom and Hendrixson, 2005a: 131; 2005b: 35; Soleglad and Fet, 2005: 4, 6, 7; Graham and Fet, 2006: 7, 8, 10; Fet et al., 2006a: 9, table 1; 2006b: 8; 2006c: 7, tables 1, 9; Soleglad and Fet, 2006: 6, 26, tables 2, 3; Graham and Soleglad, 2007: 11, 12; Soleglad et al., 2007: 134, 135.

Hoffmannius (part): Soleglad and Fet, 2008: 1, 4, 26, 34, 38, 51, 53, 54, 57, 60, 62, 66, 67, 69, 71, 73, 74, 89–92, 96, 102; Ayrey and Soleglad, 2011: 1.

Kochius (part): Soleglad and Fet, 2008: 1, 26, 57, 60, 89, 91, 94–96, 102; Ayrey and Soleglad, 2011: 1.

ETYMOLOGY: The generic name is a noun in apposition, masculine in gender, referring to the Chihuahuan Desert to which this genus is endemic.

DIAGNOSIS: Species of *Chihuahuanus*, gen. nov., may be distinguished from all other Syntropinae by the presence in adults of a small fusiform, whitish glandular area on the dorsal surface of the telson, near the base of the aculeus (fig. 26A). Species of *Maaykuyak*, gen. nov., also possess a gland on the dorsal surface of the telson, but it is larger, less defined, and situated medially (fig. 26B). The pedipalp chela fixed finger of *Chihuahuanus*, gen. nov., consistently exhibits five primary subrows of median denticles and five prolateral denticles in the median denticle row, and trichobothrium *et* is situated midway between RD3 and RD4 (fig. 17B). The carapace is shagreened, comprising coarse, rounded and fine, scattered granules in most species of *Chihuahuanus*, gen. nov. (fig. 16B).

Chihuahuanus bilineatus, comb. nov., *C. coahuilae*, comb. nov., *C. glabrimanus*, comb. nov., and *C. globosus*, comb. nov., resemble *Mesomexovis*, gen. nov., and *Paravaejovis* in the relative obsolescence of carinae on the pedipalp chela manus and metasoma (e.g., vl and vsm carinae). The pedipalp chelal carinae of *Mesomexovis*, gen. nov., and, with few exceptions, *Paravaejovis* are obsolete and smooth (fig. 19A–D), unlike the carinae of most species of *Chihuahuanus*, gen. nov., which are costate or crenulate (fig. 17A, B). The vsm carinae of metasomal segments III and IV are costate to granular, at least in the distal half, in *Chihuahuanus*, gen. nov. (fig. 27A), but obsolete and smooth in *Mesomexovis*, gen. nov., and *Paravaejovis* (fig. 27B, C), with few exceptions (e.g., *M. atenango*, comb. nov.; *M. occidentalis*, comb. nov.; *P. confusus*, comb. nov.; *P. pumilis*; and *P. waeringi*, comb. nov.). Four species of *Chihuahuanus*, gen. nov. (*C. bilineatus*, comb. nov.; *C. coahuilae*, comb. nov.; *C. glabrimanus*, comb. nov.; *C. globosus*, comb. nov.) resemble the species of *Mesomexovis*, gen. nov. (except *M. atenango*, comb. nov.) and two species of *Paravaejovis* (*P. gravicaudus*, comb. nov.; *P. spinigerus*, comb. nov.) in the extensive infuscation of the carapace, tergites, and metasoma.

INCLUDED SPECIES: *Chihuahuanus bilineatus* (Pocock, 1898), comb. nov.; *Chihuahuanus cazieri* (Williams, 1968), comb. nov.; *Chihuahuanus coahuilae* (Williams, 1968), comb. nov.; *Chihuahuanus crassimanus* (Pocock, 1898), comb. nov.; *Chihuahuanus glabrimanus* (Sissom and Hendrixson, 2005), comb. nov.; *Chihuahuanus globosus* (Borelli, 1915), comb. nov.; *Chihuahuanus kovariki* (Soleglad and Fet, 2008), comb. nov.; *Chihuahuanus russelli* (Williams, 1971), comb. nov.

DISTRIBUTION: *Chihuahuanus*, gen. nov., is endemic to the Chihuahuan Desert in Mexico (Aguascalientes, Chihuahua, Coahuila, Durango, Nuevo León, Tamaulipas, Zacatecas)

and the United States (Arizona, New Mexico, Texas; fig. 4).

NATURAL HISTORY: Species of *Chihuahuanus*, gen. nov., occur in diverse habitats including sand dunes, shrubland, and pine-oak forest, at altitudes from 530–2380 m, and have been collected under stones and on the surface at night, using UV light detecion. Although most species of the genus are lapidicolous, some species exhibit psammophilous adaptations, e.g., setal combs on the basitarsi in *C. globosus*, comb. nov. (fig. 21A), which are more developed in females.

REMARKS: This genus accommodates species previously assigned to Williams' (1970a, 1971a) *eusthenura* and *punctipalpi* groups of *Vaejovis*, many of which were originally part of Hoffmann's (1931) "first section" of that genus. Soleglad and Fet (2008) devised the names *Hoffmannius* and *Kochius* for the *eusthenura* and *punctipalpi* groups, respectively, without quantitatively testing their monophyly and composition. Both genera, as defined by Soleglad and Fet (2008), were consistently polyphyletic, and the group of species hereby assigned to *Chihuahuanus*, gen. nov., consistently monophyletic, in the phylogenetic analyses of González-Santillán and Prendini (in press) based on DNA and those based on morphology and DNA. *Chihuahuanus bilineatus*, comb. nov., *C. coahuilae*, comb. nov., *C. glabrimanus*, comb. nov., and *C. globosus*, comb. nov., were previously assigned to the *eusthenura* group (Williams, 1970a; Lourenço and Sissom, 2000; Sissom, 2000) and then to *Hoffmannius* (Soleglad and Fet, 2008); *C. cazieri*, comb. nov., *C. crassimanus*, comb. nov., and *C. russelli*, comb. nov., to the *punctipalpi* group (Williams, 1971a; Lourenço and Sissom, 2000; Sissom, 2000) and then to *Kochius* (Soleglad and Fet, 2008); and *C. kovariki*, comb. nov., to *Kochius* (Soleglad and Fet, 2008).

MATERIAL EXAMINED: *Chihuahuanus bilineatus* (Pocock, 1898), comb. nov.: **MEXICO: Tamaulipas:** *Municipio de Jaumave*: El Salto, between Palmillas and Jaumave, 23°21.4398′N 99°30.9408′W, 1115 m, 23.viii.2006, O.F. Francke, W.D. Sissom, G. Casper, T. Anton, V. Torti, H. Montaño, and C. Santibáñez, 1♂, 1♀ (CAS [ARA 1883]). *Chihuahuanus cazieri* (Williams, 1968), **comb. nov.**: **MEXICO: Coahuila:** *Municipio de Cuatro Ciénegas*: Cuatro Ciénegas de Carranza, 0.5 km S of town, 740 m, 28.vii.1967, S.C. Williams and W.S. Brown, holotype ♂ (CAS Type No. 10169); Cuatro Ciénegas de Carranza, 0.5 km SW, 740 m, 28.vii.1967, S.C. Williams and W.S. Brown, 1♂, 1♀ paratypes (AMNH). *Chihuahuanus coahuilae* (Williams, 1968), comb. nov.: **MEXICO: Coahuila:** *Municipio de Cuatro Ciénegas*: Cuatro Ciénegas de Carranza, 0.5 km SW, 740 m, 28.vii.1967, holotype ♂ (CAS Type No. 10170); Ojo de Agua, Ejido El Oso, 27°0.0558′N 102°0.2262′W, 1039 m, 19.vii.2006, O.F. Francke, W.D. Sissom, K. McWest, B. Hendrixson, S. Grant, A. Jaimes, and M. Córdova, 2♂, 2♀ (IBUNAM [ARA 84]). *Chihuahuanus crassimanus* (Pocock, 1898), comb. nov.: **MEXICO: Coahuila:** *Municipio de Cuatro Ciénegas*: Dunas de Yeso, 26°51.7650′N 102°10.47′W, 776 m, 18.vii.2006, O.F. Francke, W.D. Sissom, M. Córdova, A. Jaimes, and A. Ballesteros, 1♂ (AMNH [ARA 1105]); Sierra San Marcos II, 26°54.7998′N 102°8.25′W, 761 m, 18.vii. 2006, E. González, B. Hendrixson, K.J. McWest, and S. Grant, 1♀ (AMNH [ARA 1110]). **Durango:** *Municipio de Tlahualilo*: Tlahualilo de Zaragoza, ca. 15 km NW, junction Montes Claros–Tlahualilo de Zaragoza, 26°9.2418′N 103°31.28′W, 1107 m, 6.viii.2005, O.F. Francke, W.D. Sissom, K.J. McWest, C. Lee, H. Montaño, J. Ballesteros, and L. Jarvis, 1♂ (AMNH [ARA 3170]). **U.S.A.: Texas:** *Hudspeth Co.*: Sierra Blanca, 9 mi. W, 18.viii.1962, C.A. Triplehorn, 1♀ (OSAL). *Chihuahuanus glabrimanus* (Sissom and Hendrixson, 2005), comb. nov.: **MEXICO: Guanajuato:** *Municipio de San Diego de la Unión*: San Diego de la Unión, 8 km S, 21°23.1444′N 100°53.4522′W, 2078 m, 28.vii.2006, E. González, M. Córdova, A. Jaimes, A. Ballesteros, and O.F. Francke, 1♂ (AMNH). **San Luis Potosí:** *Municipio de Villa de Arista*: Villa de Arista, 10 km E, 22°30.760′N 100°45.499′W, 30.viii.2006, O.F. Francke, W.D. Sissom, G. Casper, T. Anton, V. Torti, H. Montaño, C. Santibáñez, and A. Ballesteros, 4♂, 1♀ (CAS [ARA 1909]). *Chihuahuanus globosus* (Borelli, 1915), comb. nov.: **MEXICO: Coahuila:** *Municipio de Cuatro Ciénegas*: Gypsum dunes, 13 km SW Cuatro Ciénegas de Carranza, 780 m, 27.vii.1967, S.C. Williams

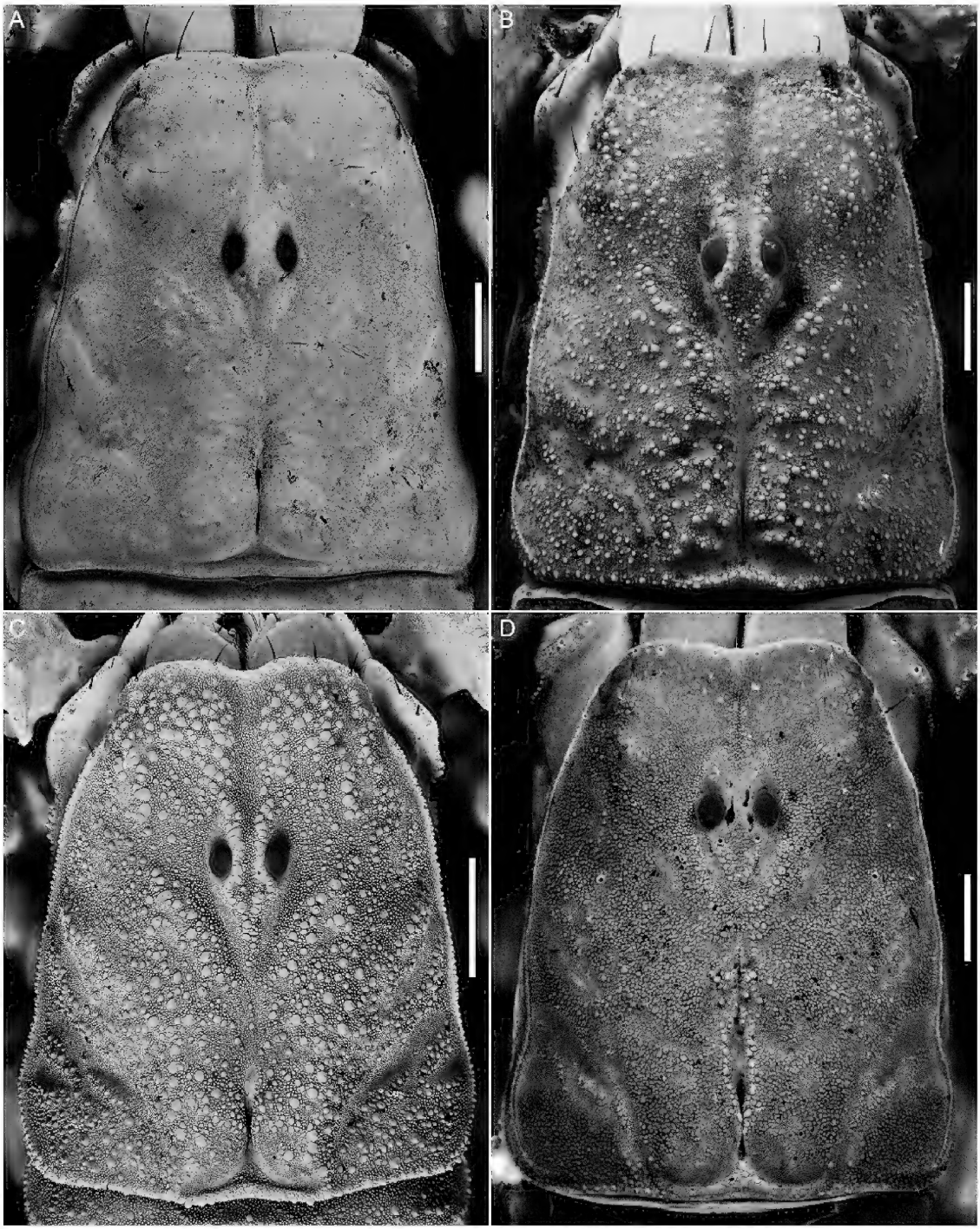


Fig. 16. Syntropinae Kraepelin, 1905, carapace, dorsal aspect, illustrating surface ornamentation. **A.** *Balsateres cisnerosi* (Ponce-Saavedra and Sissom, 2004), comb. nov., ♂ (IBUNAM). **B.** *Chihuahuanus crassimanus* (Pocock, 1898), comb. nov., ♂ (AMNH). **C.** *Kochius bruneus* (Williams, 1970), ♂ (AMNH). **D.** *Konetontli acapulco* (Armas and Martín-Frías, 2001), comb. nov., holotype ♂ (IBUNAM). Scale bars = 1 mm (**A–C**), 0.5 mm (**D**).

and W.S. Brown, holotype ♂ of *Vaejovis gilvus* Williams, 1968 (CAS Type No. 10172). *Municipio de Cuatro Ciénegas*: Cuatro Ciénegas, 16 mi. SW, W point of Laguna Grande dunes, 9.viii.1968, S.C. Williams, M. Bentzien, J. Bigelow, and W.L. Minckley, 1♂, 1♀ (AMNH). *Municipio de Viesca*: Dunas de Bilbao, 25°25.5858′N 102°53.6538′W, 1098 m, 20.vii.2006, O.F. Francke, K.J. McWest, M. Córdova, A. Jaimes, and A. Ballesteros, 4♂, 1♀ (CAS [ARA 1879]). *Chihuahuanus kovariki* (Soleglad and Fet, 2008), comb. nov.: **MEXICO: Durango:** *Municipio de San Juan del Río*: Hwy 137, marker km 4, between Once de Marzo and San Juan del Río, San Francisco de Lajas, 24°51.764′N 104°38.846′W, 1893 m, 10.viii.2005, O.F. Francke, W.D. Sissom, K.J. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis, and C. Durán, 1♂ (AMNH). Yerbanis, 80 mi. NW Durango, 19.viii.1947, W.J. Gertsch, 1♀ (AMNH). *Chihuahuanus russelli* (Williams, 1971), comb. nov.: **U.S.A.: Arizona:** *Cochise Co.*: Portal, 4770 ft, 26.viii.1965, S.C. Williams and G. Fernald, holotype ♂ (CAS Type No. 11471). **New Mexico:** Rodeo, 10 mi. N, 22.ix.1963, V. Roth, 1♀ (AMNH). **Texas:** *Brewster Co.*: Big Bend National Park, Pine Canyon Trail, Chisos Mountains, 29.2678°N 103.2371°W, 1.viii.2008, W.D. Sissom, G. Casper, and T. Anton, 2♂ (AMNH).

Kochius Soleglad and Fet, 2008
Figures 1B, 2B, 5, 7, 9–11, 16C, 18A, B, 22A, 23A, 24A, 25A; table 1

Buthus punctipalpi Wood, 1983 [= *Kochius punctipalpi* (Wood, 1983)], type species, by original designation.

Vaejovis punctipalpi group (part): Williams, 1971a: 37; 1971b: 44; 1980: 80; Sissom and Francke, 1985: 1; Sissom, 1989: 180; 1991: 26; Stockwell, 1992: 408, 409; Sissom, 1993: 68; Lourenço and Sissom, 2000: 135; Sissom, 2000: 532, 548, 551; Armas and Martín-Frías, 2001: 1; Hendrixson, 2001: 1; Ponce-Saavedra and Sissom, 2004: 539, 541; Sissom and Hendrixson, 2005a: 131; 2005b: 35; Soleglad and Fet, 2005: 4, 6, 7; Graham and Fet, 2006: 7, 8, 10; Fet et al., 2006a: 9, table 1; 2006b: 8; 2006c: 7; Soleglad and Fet, 2006: 6, 26, tables 2, 3; Graham and Soleglad, 2007: 11, 12; Francke and González-Santillán, 2007: 586, 587, 590; Soleglad et al., 2007: 134, 135; Soleglad and Fet, 2008: 1, 26, 57, 60, 94, 95, 102; McWest, 2009: figs. 322–326, tables 1, 53, 89, 91, 93, 101–105, 108, 123.

Kochius Soleglad and Fet, 2008: 1, 3, 34, 38, 51, 53, 54, 57, 58, 60–69, 71, 73, 74, 76, 79, 91–96, 102, 104, figs. 192, 193–196, 204, tables 2, 4, 6, 9 (part); Ayrey and Soleglad, 2011: 1 (part).

DIAGNOSIS: *Kochius* differs from all other genera of Syntropinae in possessing the longest macrosetae on the telson vesicle of the female and, in some species, of both sexes (fig. 25A); some macrosetae are as long as or longer than the aculeus, becoming narrower and translucent terminally. Species of *Kochius* are also characterized by a raised, whitish boss, restricted to the posteromedial third of mesosomal sternite VII (fig. 23A). Although other genera of Syntropinae possess whitish glandular surfaces on sternite VII (fig. 23B), the structure in *Kochius*, which is noticeably more elevated and usually shaped like a truncate triangle, is unique. Most Syntropinae also display a glandular surface posteromedially on sternite V, but it is more pronounced in *Kochius* (fig. 23A). Additional diagnostic characters of *Kochius* are as follows. Species of *Kochius* possess more pronounced, granular carinae on the pedipalp chela manus, especially the drs, drsa, and rlm carinae (fig. 18A, B), and the pedipalp patellar rlds and rlm carinae are more coarsely granular than in other genera of Syntropinae. The pedipalp carinae of *Kochius* are also distinctive in comprising moniliform granules (fig. 18A, B), rather than clustered granules, as in other genera (fig. 17A–D). The patellar dorsal intercarinal surface (between the dpl and drl carinae) is flat in *Kochius*, compared to other genera in which it is slightly concave. The densely and coarsely granular (shagreened) carapace (fig. 16C), markedly shagreened mesosomal posttergites I–VII and sternite VII (fig. 23A), and uniformly finely granular (matte) ventral intercarinal surfaces of the pedipalp chela manus, retrolateral intercarinal surfaces of the pedipalp patella and intercarinal surfaces of metasomal segments I–V (fig. 24A) are also characteristic for the genus. Pedipalp chela trichobothrium *esb* is situated at RD6 and/or its associated macroseta, and trichobothrium *Db* is situated dorsal to the drl carina, compared with *Paravaejovis*, in which *esb* is situated between RD6 and RD5 (fig. 19D), and *Mesomexovis*, gen. nov., in

which *Db* is situated on the drl carina (fig. 19A). The macrosetae of legs I–IV also tend to be shorter and stouter in *Kochius* than in other genera (fig. 22A).

Four species of *Chihuahuanus*, gen. nov. (*C. cazieri*, comb. nov., *C. crassimanus*, comb. nov., *C. kovariki*, comb. nov., and *C. russelli*, comb. nov.) resemble *Kochius* in possessing a raised, whitish boss in the posteromedial third of mesosomal sternite VII (fig. 23A), but may be separated from the latter by the small fusiform, whitish glandular area, anterior to the base of the aculeus, on the dorsal surface of the telson vesicle of adults; the shorter macrosetae on the telson vesicle of females; the less-developed (lower and smoother) pedipalp chelal rlm and rlvs carinae, and patellar rlds and rlm carinae; and the clustered instead of moniliform granules of the pedipalp carinae.

Species of *Thorellius* resemble *Kochius* with respect to the incrassate pedipalp chela manus and generally pronounced carination of the manus, especially the markedly granular rlm and rlvs carinae (figs. 17C, D, 18A, B), and metasoma, but can be separated from the latter by their considerably larger size and by the clustered instead of moniliform granules of the pedipalp carinae.

INCLUDED SPECIES: *Kochius barbatus* (Williams, 1971), stat. nov.; *Kochius bruneus* (Williams, 1970); *Kochius cerralvensis* (Williams, 1971), stat. nov.; *Kochius insularis* (Williams, 1971); *Kochius hirsuticauda* (Banks, 1910); *Kochius magdalensis* (Williams, 1971); *Kochius punctipalpi* (Wood, 1863); *Kochius sonorae* (Williams, 1971); *Kochius villosus* (Williams, 1971), stat. nov.

DISTRIBUTION: *Kochius* is endemic to Mexico (recorded from Baja California, Baja California Sur, and Sonora) and the United States (recorded from Arizona, California, and Nevada; fig. 5). All except *K. hirsuticauda* and *K. sonorae*, occurring in the Mojave and Sonoran (including Colorado) deserts on the North American mainland, are endemic to the Baja California Peninsula and adjacent islands.

NATURAL HISTORY: Species of *Kochius* inhabit desert to semidesert habitats from sea level to 1350 m altitude. They have been collected under stones or other available debris on the ground, and on the surface at night, with UV light detection. Although Sissom (2000) suggested that these scorpions are burrowers, the absence of fossorial adaptations suggests otherwise. The cheliceral fingers are not enlarged, the pedipalp chela fingers are fairly slender, the tarsi are not laterally compressed and lack setal combs, and the metasoma lacks enlarged carinal processes and lobes. The habitat and habitus of *Kochius* are consistent with the lapidicolous ecomorphotype (Prendini, 2001a).

REMARKS: As redefined here, this genus accommodates species previously assigned only to Williams' (1971a) *punctipalpi* group of *Vaejovis*, for which Soleglad and Fet (2008) devised the name *Kochius*, without quantitatively testing its monophyly or composition. *Kochius*, as defined by Soleglad and Fet (2008), was consistently polyphyletic, and the group of species hereby assigned to it consistently monophyletic, in the phylogenetic analyses of González-Santillán and Prendini (in press) based on morphology and those based on morphology and DNA. The following species are therefore transferred to other genera in the present contribution: *Mesomexovis atenango*, comb. nov., previously assigned to the *punctipalpi* group (Francke and González-Santillán, 2007) and then to *Kochius* (Soleglad and Fet, 2008); *C. cazieri*, comb. nov., *C. crassimanus*, comb. nov., and *C. russelli*, comb. nov., previously assigned to the *punctipalpi* group (Williams, 1971a, b; Sissom, 2000) and then to *Kochius* (Soleglad and Fet, 2008); *C. kovariki*, comb. nov., previously assigned to *Kochius* (Soleglad and Fet, 2008).

The analyses of González-Santillán and Prendini (in press) identified sufficient, consistent diagnostic character differences to elevate to the rank of species, *K. barbatus*, stat. nov., and *K. cerralvensis*, stat. nov., previously considered subspecies of *K. punctipalpi*, and *K. villosus*, stat. nov., previously considered a subspecies of *K. bruneus* (Williams, 1971a, 1980; Sissom, 2000). *Vaejovis bruneus loretoensis* Williams, 1971, was not found to differ consistently from *K. villosus*, stat. nov., with which it is hereby synonymized: *Vaejovis bruneus loretoensis* Williams, 1971 = *Kochius villosus* (Williams, 1971), syn. nov.

MATERIAL EXAMINED: *Kochius barbatus* (Williams, 1971), stat. nov.: **MEXICO: Baja**

California Sur: *Municipio de La Paz*: Las Cruces, 25 ft, 29.vii.1968, S.C. Williams and M.A. Cazier, holotype ♀ of *Vaejovis punctipalpi barbatus* Williams, 1971 (CAS Type No. 10469), paratype ♀ (AMNH); Las Cruces, 4 km NW, 24°13.5108′N 110°7.41′W, 31 m, 24.vi.2008, H. Montaño and E. González, 1♂ (AMNH [ARA 2884]), 1♂ (IBUNAM [ARA 2274]). *Kochius bruneus* (Williams, 1970): **MEXICO: Baja California Sur:** *Municipio de Comondú*: San José de Comondú, 5 mi. SW, 1000 ft, 2.vii.1968, S.C. Williams and M.A. Cazier, holotype ♂ (CAS Type No. 10410); San José de Comondú, 30 km N, between Rosarito and San Isidro, 26°21.2520′N 111°50.10′W, 258 m, 27.vi.2008, H. Montaño and E. González, 2♂, 2♀ (AMNH [ARA 2854]). *Kochius cerralvensis* (Williams, 1971), stat. nov.: **MEXICO: Baja California Sur:** *Municipio de La Paz*: Isla Cerralvo, Bahía Limona, 31.v.1969, S.C. Williams, holotype ♂ (CAS Type No. 11470); Isla Cerralvo, Piedras Gordas, 17.v.1970, S.C. Williams and V.F. Lee, 1♂, 1♀ paratypes (AMNH); Isla Cerralvo, SW side, 24°10.9332′N 109°53.2332′W, 50 m, 27.v.2008, E. González and I.G. Nieto, 1♂, 1♀ (AMNH [ARA 2880]). *Kochius hirsuticauda* (Banks, 1910): **U.S.A.: Arizona:** *Yuma Co.*: Palm Canyon, Kofa Mountains, 12.x.1968, M.A. Cazier et al., 1♂, 1♀ (AMNH). **California:** *San Diego Co.*: Anza-Borrego Desert State Park: Pinyon Mountain Road, ca. 4.8 km towards Pinyon Mountain Valley from junction with Route S2, 33°03.043′N 116°23.270′W, 870 m, 30.viii.2005, R. Mercurio and L. Prendini, 1♂, 1♀ (AMNH). *Kochius insularis* (Williams, 1970): **MEXICO: Baja California Sur:** *Municipio de La Paz*: Isla Partida, Central Valley, 10.vii.1968, S.C. Williams, M. Bentzien, and B. Fox, holotype ♂ (CAS Type No. 10422), allotype ♀ (CAS). *Municipio de La Paz*: Isla Espíritu Santo, Playa Bonanza, 24°27.3636′N 110°18.47′W, 50 m, 31.v.2008, E. González and I.G. Nieto, 1♂, 1♀ (AMNH [ARA 2875]), 1♂, 1♀ (IBUNAM [ARA 2260]). *Kochius magdalensis* (Williams, 1971): **MEXICO: Baja California Sur:** *Municipio de La Paz*: La Paz, 75 mi. NW, 200 ft, 4.vii.1968, S.C. Williams and M.A. Cazier, holotype ♂ (CAS Type No. 10468); El Pilar, ca. 20 km NE Las Pocitas, 24°28.7616′N 111°1.12′W, 92 m, 25.vi.2008, H. Montaño and E. González, 1♂, 1♀ (AMNH [ARA 2874]), 1♂, 1♀ (IBUNAM [ARA 2259]); Junction Route 1 and road to Juan de la Costa, 5 km N, 24°08.500′N 110°28.566′W, 30 m, 9.vi.2005, E. González, W.E. Savary, R. Mercurio, and L. Prendini, 1♂ (AMNH). *Kochius punctipalpi* (Wood, 1863): **MEXICO: Baja California Sur:** *Municipio de Los Cabos*: Santiago, 23°26.4′N 109°43.5666′W, 225 m, 9.vii.2004, O.F. Francke, E. González, and A. Valdez, 1♂, 1♀ (AMNH [ARA 1471]); San José del Cabo, ca. 10 km S off Route 1, 23°1.7622′N 109°43.49′W, 50 m, 10.vii.2005, W.E. Savary, E. González, and R. Mercurio, 1♂, 1♀ (AMNH [ARA 1473]). *Municipio de La Paz*: La Paz, 15 km SE, 24°3.7332′N 110°10.53′W, 476 m, 8.vii.2004, O.F. Francke, E. González, and A. Valdez, 1♂ (AMNH [ARA 1472]). *Kochius sonorae* (Williams, 1971): **MEXICO: Sonora:** *Municipio de Alamos*: Alamos, 11.2 mi. W, 23.i.1966, R. Winokur, C. Mays, and M.A. Nikerson, holotype ♂ (CAS Type No. 10472). *Municipio de Navojoa*: Microwave antenna Cerro Prieto, 15 km E Navojoa, 27°4.9830′N 109°17.4498′W, 375 m, 23.viii.2009, E. González and J.L. Castelo, 1♂, 1♀ (AMNH [ARA 3157]); Navojoa, 32 km S, 12.ix.1966, J. and W. Ivie, 1♂, 1♀ (AMNH). *Municipio de Soyopa*: Sierra el Encinal, 9 km from Hwy MEX 16 on dirt road to El Encinal, 28°35.4120′N 109°27.1476′W, 380 m, 24.vi. 2006, E. González and P. Berea, 2♂ (AMNH [ARA 2539]); dirt road between El Encinal and Tonichi, 28°33.2388′N 109°21.64′W, 645 m, 1.vii.2006, E. González and P. Berea, 2♂ (AMNH [ARA 3015]). *Kochius villosus* (Williams, 1971), stat. nov.: **MEXICO: Baja California Sur:** *Municipio de Comondú*: San Miguel Comondú, 5–10 mi. SW, 800–1000 ft, 3.vii.1968, S.C. Williams and M.A. Cazier, holotype ♂ of *Vaejovis bruneus villosus* Williams, 1971 (CAS Type No. 10467), 1♂, 1♀ paratypes (AMNH). *Municipio de La Paz*: San Evaristo, 10–15 km S, dirt road, 24°47.7570′N 110°40.5018′W, 50 m, 12.vii.2008, H. Montaño and E. González, 1♂ (IBUNAM [ARA 2275]), 1♂, 1♀ (AMNH [ARA 2888]). *Municipio de Loreto*: Juncalito, 25°49.8918′N 111°19.6908′W, 5 m, 20.v.2004, R. Mercurio and M. Nishiguchi, 1♂, 1♀ (AMNH [ARA 3132]). *Municipio de Mulegé*: San Ignacio, 152 m, 24.vi.1968, S.C. Williams

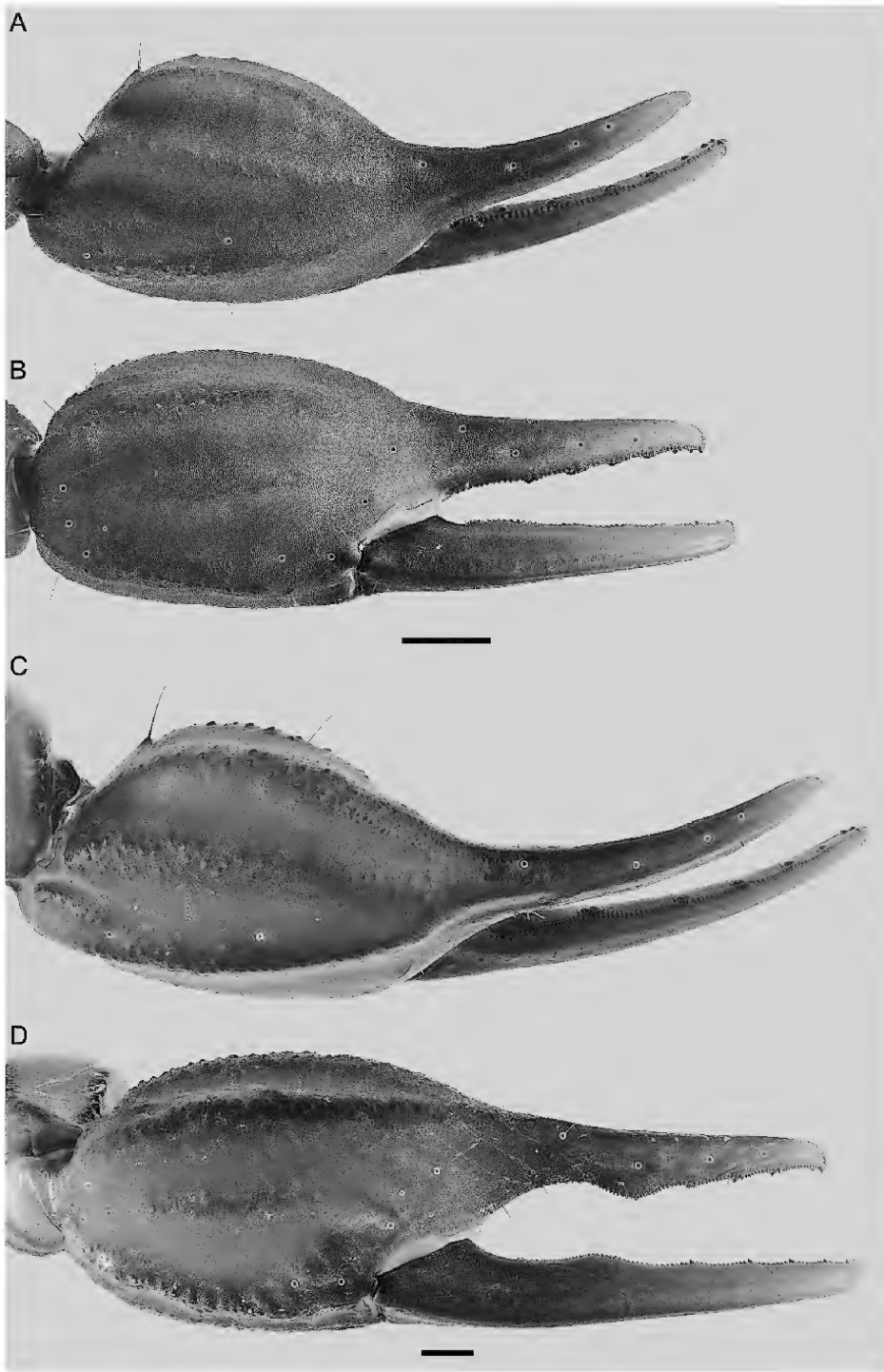


Fig. 17. Syntropinae Kraepelin, 1905, dextral pedipalp chela, dorsal (**A, C**) and retrolateral (**B, D**) aspects, illustrating carinae and distribution of trichobothria. **A, B.** *Chihuahuanus crassimanus* (Pocock, 1898), comb. nov., ♂ (AMNH). **C, D.** *Thorellius intrepidus* (Thorell, 1876), ♂ (AMNH). Scale bars = 1 mm.

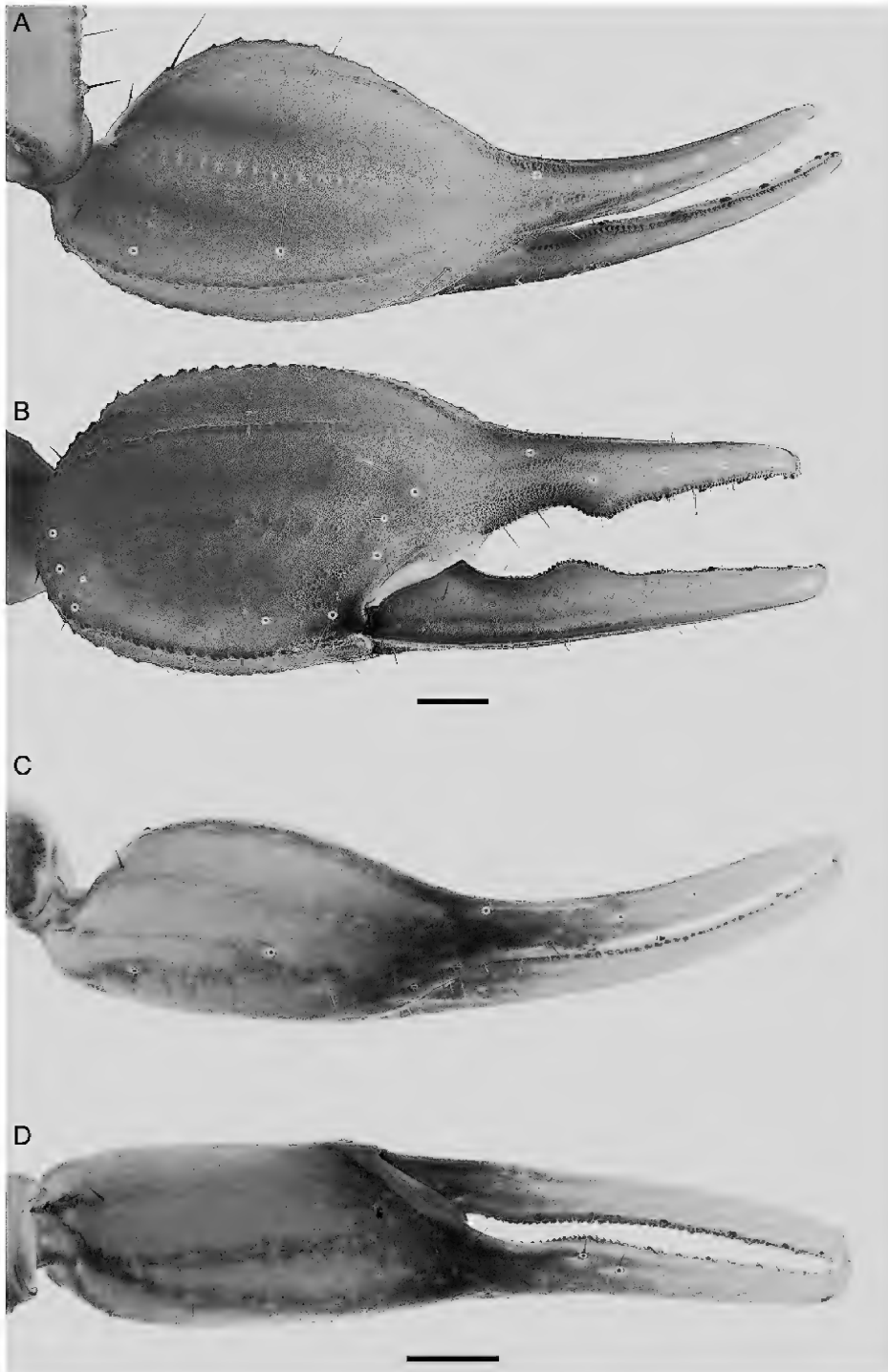


Fig. 18. Syntropinae Kraepelin, 1905, dextral pedipalp chela, dorsal (**A, C**), retrolateral (**B**) and prolateral (**D**) aspects, illustrating carinae and distribution of trichobothria. **A, B.** *Kochius punctipalpi* (Wood, 1863), ♂ (AMNH). **C, D.** *Kuarapu purhepecha* Francke and Ponce-Saavedra, 2010, paratype ♂ (AMNH). Scale bars = 1 mm (**A, B**), 0.5 mm (**C, D**).

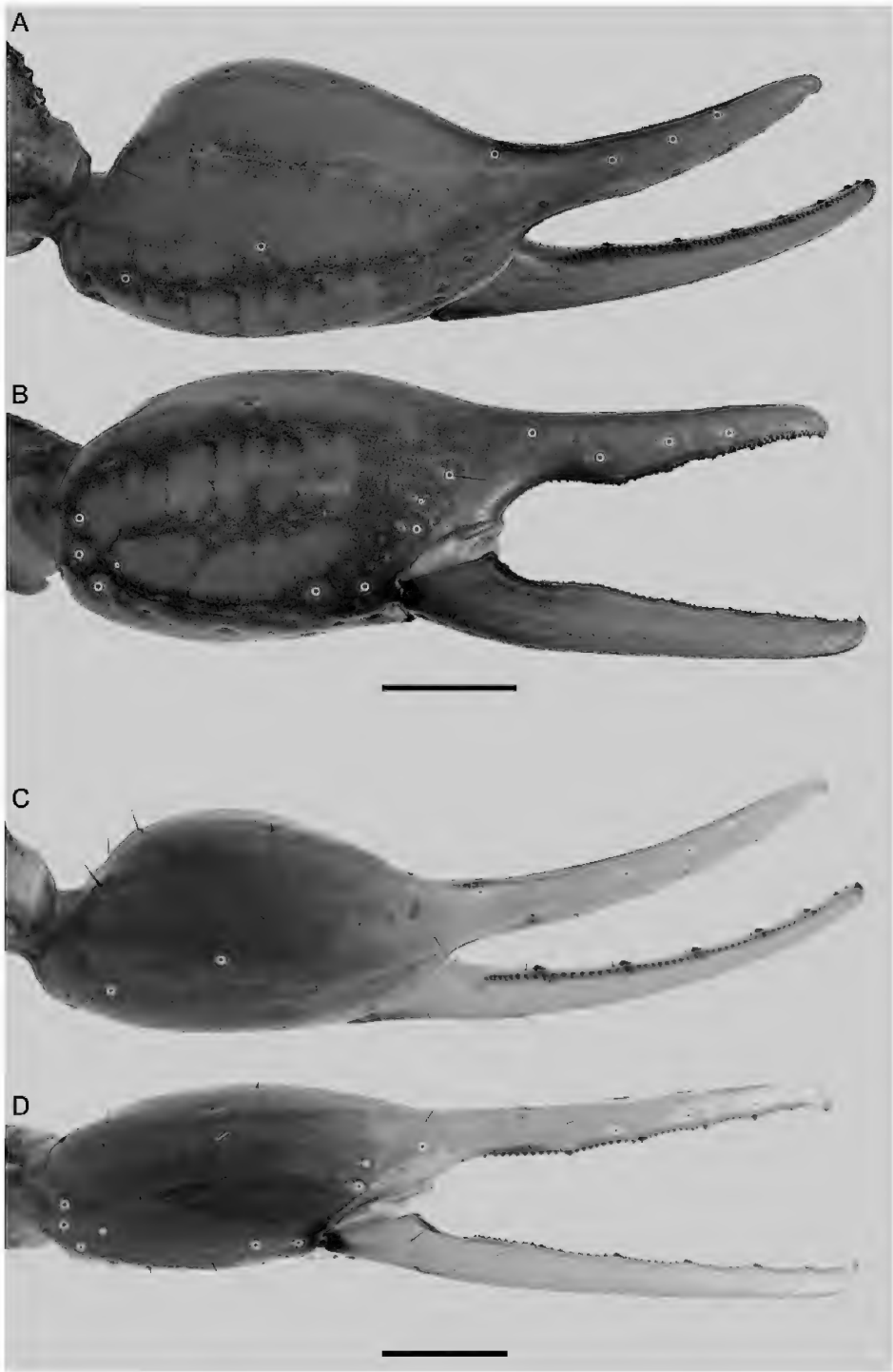


Fig. 19. Syntropinae Kraepelin, 1905, dextral pedipalp chela, dorsal (**A, C**) and retrolateral (**B, D**) aspects, illustrating carinae and distribution of trichobothria. **A, B.** *Mesomexovis punctatus* (Karsch, 1879), comb. nov., ♂ (AMNH). **C, D.** *Paravaejovis hoffmanni* (Williams, 1970), ♂ (AMNH). Scale bars = 1 mm.

and M.A. Cazier, holotype ♂ of *V. b. loretoensis* (CAS Type No. 10466), allotype ♀, 1 ♂, 1 ♀ paratypes (AMNH).

Konetontli, gen. nov.
Figures 4, 7, 15A–C, 16D, 25B, C, 28B; table 1

Vaejovis pattersoni Williams and Haradon in Williams, 1980 [= *Konetontli pattersoni* (Williams and Haradon in Williams, 1980), comb. nov.], type species, here designated.

Vaejovis eusthenura group (part): Williams, 1980: 65, figs. 56F, 69, 75, tables 1, 2; 1986: 358; Sissom, 2000: 530, 531; Francke and Ponce-Saavedra, 2005: 67.

Vaejovis mexicanus group (part): Sissom 2000: 542; Soleglad and Fet, 2008: 1, 2, 5, 13, 26, 37, 40, 46, 71, 73, 89, 99, 100, figs. 126, 196, 207, tables 2, 9.

ETYMOLOGY: The generic name is a noun in apposition, masculine in gender, taken from the Nahuatl language, meaning "infant" or "small creature," and referring to the small adult body size of the species in this genus.

DIAGNOSIS: *Konetontli*, gen. nov., differs from all other genera of Syntropinae in the presence of a spiniform subaculear tubercle, slightly compressed laterally with a rounded tip, and sometimes associated with smaller accessory tubercles situated anteriorly along the vm carina of the telson vesicle (fig. 25B, C). Additional diagnostic characters of the genus are as follows. Species of *Konetontli*, gen. nov., are very small, with total body length (adult) 14–25 mm. The tergites are entirely infuscated and most of the integument uniformly finely granular (matte; fig. 16D). Pedipalp chela trichobothrium *it* is situated between RD6 and the macroseta situated at the position of RD7 (which is absent), and trichobothrium *ib* proximal to the macroseta at the position of RD7. Metasomal segments I, II, and, in some cases, III are wider than long. The vl carinae of metasomal segment V are obsolete to absent in several species.

Konetontli, gen. nov. shares with *Kuarapu*, *Maaykuyak*, gen. nov., *Syntropis*, *Vizcaino*, gen. nov., *Chihuahuanus bilineatus*, comb. nov., *C. coahuilae*, comb. nov., and *Thorellius cristimanus* the presence of a secondary hook on the hemispermatophore, created by an extension of the axial carina of the distal lamina, that forms a pronounced bifurcation with the primary hook.

Konetontli, gen. nov., resemble *Mesomexovis*, gen. nov., in the dense infuscation of the carapace and sternites I–VII, and the partially to completely infuscate mesosomal sternite VII, but adults of *Mesomexovis*, gen. nov., are much larger. *Konetontli*, gen. nov., shares with *Maaykuyak waueri*, comb. nov., and *P. pumilis* a single pair of ventrodistal spinules on the telotarsi (fig. 22B, C). However, both *M. waueri*, comb. nov., and *P. pumilis* are separated from *Konetontli*, gen. nov., by the absence of a subaculear tubercle, and *P. pumilis* further by the neobothriotaxic pedipalp chela and uniformly pale, immaculate coloration.

INCLUDED SPECIES: *Konetontli acapulco* (Armas and Martín-Frías, 2001), comb. nov.; *Konetontli chamelaensis* (Williams, 1986), comb. nov.; *Konetontli kuarapu* (Francke and Ponce-Saavedra, 2005), comb. nov.; *Konetontli nayarit* (Armas and Martín-Frías, 2001), comb. nov.; *Konetontli pattersoni* (Williams and Haradon in Williams, 1980), comb. nov.

DISTRIBUTION: *Konetontli*, gen. nov., is endemic to Mexico and recorded from six states: Baja California Sur, Colima, Guerrero, Jalisco, Michoacán, and Nayarit (fig. 4). This genus has a disjunct distribution: *Konetontli pattersoni*, comb. nov., inhabits the Cape region of the Baja California Peninsula, isolated from the other four species on the Mexican mainland by the Gulf of California. The mainland species are distributed along the Pacific coast, Sierra Madre del Sur, and the Balsas Depression.

NATURAL HISTORY: The species of *Konetontli*, gen. nov., from mainland Mexico inhabit tropical deciduous forest from sea level to 936 m altitude, unlike *K. pattersoni*, comb. nov., which inhabits pine-oak forest from 850–1800 m in the Sierra de la Laguna, Baja California Sur. Described species for which habitat data are available, were mostly collected under rocks and other debris, in areas with a dense layer of leaf litter (Armas and Martín-Frías, 2001; Baldazo-Monsivais, 2003; González-Santillán, 2004), whereas two undescribed species were collected inside caves, in all cases suggesting a requirement for high relative humidity. The very small size

and cryptic coloration of these scorpions, taken together with available habitat data, are consistent with the humicolous and lapidicolous ecomorphotypes (Prendini, 2001a).

REMARKS: The species of *Konentontli*, gen. nov., are united, among other characters, by the possession of a subaculear tubercle on the telson, an uncommon character among vaejovid scorpions. Only eight vaejovids with a subaculear tubercle have been described to date (Haradon, 1974; Williams, 1980, 1986; Sissom, 1993; Armas and Martín-Frías, 2001; Baldazo-Monsivais, 2003; Francke and Ponce-Saavedra, 2005; Webber et al., 2012). Although the subaculear tubercle at first offered a potential diagnostic synapomorphy, Sissom (1993) noted that *Vaejovis mumai* Sissom, 1993, and *Vaejovis spicatus* Haradon, 1974, appeared to be more closely related to *Serradigitus* than to the other species with a subaculear tubercle, deferring a decision pending further analysis. Soleglad and Fet (2008) subsequently created *Wernerius* to accommodate the latter two species (a third was added by Webber et al., 2012), retaining the others in *Vaejovis* (i.e., the *mexicanus* group, the paraphyletic assemblage that remained after "new" names were assigned to the other putatively monophyletic groups). Not all previous authors considered these species related to members of the *mexicanus* group, however. Williams (1980, 1986) placed *Vaejovis pattersoni* and *Vaejovis chamelaensis* Williams, 1986, in the *eusthenura* group. Sissom (2000: 542) retained *V. chamelaensis* in the *eusthenura* group but transferred *V. pattersoni* to the *mexicanus* group based on the opinion "that it is closely related to members of the *mexicanus* group (e.g., *V. granulatus* Pocock) from mainland Mexico." The species described subsequently by Armas and Martín-Frías (2001), Baldazo-Monsivais (2003), and Francke and Ponce-Saavedra (2005) were also placed in the *mexicanus* group by Soleglad and Fet (2008), without testing their phylogenetic position or possible relationship to *Hoffmannius*, the "new" name proposed for Williams' (1970a) *eusthenura* group.

The species hereby assigned to *Konetontli*, gen. nov., were consistently monophyletic in the phylogenetic analyses of González-Santillán and Prendini (in press) based on morphology, and those based on morphology and DNA. These species were not related to the exemplar species of the *mexicanus* group or *Wernerius* included in the analyses, forming a monophyletic group with *Maaykuyak*, gen. nov., instead (fig. 7). The creation of a new genus for these species is based on their phylogenetic position and unique, diagnostic character combination. The subaculear tubercle appears to have evolved at least twice among Vaejovidae, in *Wernerius* and *Konetontli*, gen. nov., respectively.

MATERIAL EXAMINED: *Konetontli acapulco* (Armas and Martín-Frías, 2001), comb. nov.: **MEXICO: Guerrero:** *Municipio de Acapulco*: Colonia Francisco Villa, Acapulco, 25.v.1999, E. Martín and A. Losoya, holotype ♂ (IBUNAM). *Municipio de José Azueta*: Colonia Agua de Correa, 17°38.6982′N 101°31.0932′W, 72 m, 1.viii.2008, O.F. Francke, H. Montaño, J. Ponce, and A. Quijano, 1♀ (IBUNAM). *Konetontli chamelaensis* (Williams, 1986), comb. nov.: **MEXICO: Jalisco:** *Municipio de La Huerta*: Estación de Biología de Chamela, UNAM, 10–13.vii.1985, S.C. Williams, holotype ♂ (CAS Type No. 15744), allotype ♀ (CAS), 31.v.1990, N. Martínez, 1♀ (IBUNAM), 1.vi.1994, N. Martigera, 1♀ (IBUNAM); 19°29.875′N 105°02.608′W, 97 m, 24.x.2005, E. González and J.L. Castelo, 2♂ (IBUNAM), 30.viii.2007, O.F. Francke et al., 1♀ (AMNH [LP 7675]); Rincón de Ixtlán, Chamela, 19°32′N 105°04′W, 25.x.2005, E. González, 1♀ (IBUNAM). *Konetontli kuarapu* (Francke and Ponce-Saavedra, 2005), comb. nov.: **MEXICO: Michoacán:** *Municipio de Parácuaro*: El Valle, 19°8.8488′N 102°13.2228′W, 21.x.2000, J. Ponce et al., 1♂ (AMNH), 1♀ (IBUNAM). *Konetontli nayarit* (Armas and Martín-Frías, 2001), comb. nov.: **MEXICO: Nayarit:** *Municipio de Compostela*: Felipe Carrillo Puerto, 4 km NE, 16.vii.1999, J.A. Fernández, holotype ♂ (IBUNAM). *Municipio de El Nayar*: Río Santiago, 16.v.1996, E. Barrera, 1♀ (IBUNAM). *Konetontli pattersoni* (Williams and Haradon in Williams, 1980), comb. nov.: **MEXICO: Baja California Sur:** *Municipio de Los Cabos*: La Laguna, Sierra de la Laguna, 1–3.viii.1974, R.M. Haradon, V.F. Lee, and W.E. Savary, holotype ♂ (CAS Type

Fig. 20. Syntropinae Kraepelin, 1905, dextral pedipalp chela movable finger, dorsal aspect, illustrating dentition. **A.** *Balsateres cisnerosi* (Ponce-Saavedra and Sissom, 2004), comb. nov., ♂ (IBUNAM). **B.** *Thorellius intrepidus* (Thorell, 1876), ♂ (AMNH). **C.** *Vizcaino viscainensis* (Williams, 1970), comb. nov., ♂ (AMNH). Scale bars = 0.5 mm.

No. 12250), allotype ♀ (CAS); Sierra de la Laguna, 23°41.1666′N 109°56.6832′W, 850 m, 9.vii.2004, A. Valdez and E. González, 1♀ (AMNH [ARA 3083]); 23°14.2848′N 109°57.1314′W, 782 m, 10.vii.2004, A. Valdez, E. González, O.F. Francke, and W.E. Savary, 1♀ (AMNH [ARA 3082]); Sierra de la Laguna, nucleus zone, 23°33.0162′N

109°59.4498′W, 1800 m, 20.vii.2006, A. Valdez, E. González, O.F. Francke, and W.E. Savary, 2♂ (AMNH [ARA 3064]).

Kuarapu Francke and Ponce-Saavedra, 2010
Figures 4, 7, 18C, D, 24B; table 1

Kuarapu purhepecha Francke and Ponce-Saavedra, 2010, type species, by monotypy.
Kuarapu Francke and Ponce-Saavedra, 2010: 52; Ayrey and Soleglad, 2011: 1.

DIAGNOSIS: The following combination of characters differentiates *Kuarapu* from other genera of Syntropinae. The integument is markedly infuscate, especially on the dorsal surface of the cheliceral manus, the dm carinae of the tergites, the dorsal and ventral surfaces of the metasoma, and the ventral surface of the telson. The carapace anteromedial margin is straight and the median ocular tubercle shallow, protruding slightly, with the superciliary carinae lower than the ocelli. The carinae of the pedipalp chela manus are absent or obsolete (fig. 18C, D). The median denticle row of the pedipalp chela movable finger comprises five primary subrows of median denticles and five retrolateral denticles, and the terminal denticle of the fixed and movable fingers is larger than the preceding denticles (fig. 18C, D), but not hooklike, as in *Serradigitus*, for example. The intercarinal surfaces of metasomal segments I–V are entirely and uniformly, finely granular (matte; fig. 24B).

Kuarapu shares with the closely related genera, *Kochius* and *Thorellius*, the medial position of trichobothrium *Dt* on the pedipalp chela manus, and further resembles *Kochius* in the presence of a raised, whitish boss, restricted to the posteromedial third of mesosomal sternite VII, and the finely granular vsm and vl carinae of metasomal segments I–IV. Unlike these genera, however, both of which exhibit a generally robust habitus with incrassate, strongly carinate pedipalp chelae, the habitus of *Kuarapu* is gracile and attenuate, the chelae slender, elongated, and largely acarinate (fig. 18C, D).

Kuarapu also resembles *Vizcaino*, gen. nov., in possessing elongate pedipalp chela fingers, with fixed finger trichobothrium *it* situated between PD5 and PD6, and *ib* situated at PD6 (fig. 18D). *Kuarapu* differs from *Vizcaino*, gen. nov., in having a markedly infuscate integument, and separate rows of dorsal and retrodorsal macrosetae on the basitarsi of legs I–III. The integument is immaculate, and the dorsal and retrodorsal macrosetae are arranged in a sublinear row (forming setal combs) on the basitarsi of legs I–III, in *Vizcaino*, gen. nov. (fig. 21C).

Kuarapu shares with *Konetontli*, gen. nov., *Maaykuyak*, gen. nov., *Syntropis*, *Vizcaino*, gen. nov., *Chihuahuanus bilineatus*, comb. nov., *C. coahuilae*, comb. nov., and *Thorellius cristimanus* the presence of a secondary hook on the hemispermatophore, created by an extension of the axial carina of the distal lamina, that forms a pronounced bifurcation with the primary hook.

INCLUDED SPECIES: *Kuarapu purhepecha* Francke and Ponce-Saavedra, 2010.

DISTRIBUTION: *Kuarapu* is endemic to the Balsas Depression in the state of Michoacán, Mexico (fig. 4) and known only from the type locality.

NATURAL HISTORY: The type locality of this monotypic genus occurs in tropical deciduous forest at an altitude of 248 m. The known specimens were collected with UV light detection at night, on the surfaces of road-cuts (Francke and Ponce-Saavedra, 2010). The habitat and habitus of *Kuarapu*, especially the dorsoventral compression of the body, slender, elongated pedipalps, well-developed superciliary carinae of the medial ocular tubercle, and the tarsal morphology, are consistent with the lithophilous ecomorphotype (Prendini, 2001a). *Kuarapu* appears to have converged on this ecomorphotype with three other, unrelated groups of vaejovid scorpions: the monophyletic group comprising *Gertschius*, *Serradigitus*, *Stahnkeus*, and *Wernerius*; *Syntropis*; and the former *nitidulus* group of *Vaejovis*, presently comprising species assigned to *Franckeus* and the *nigrescens* "group" of *Vaejovis*.

MATERIAL EXAMINED: *Kuarapu purhepecha* Francke and Ponce-Saavedra, 2010: **MEXICO: Michoacán:** *Municipio de La Huacana*: El Vado, 17 km on road Zicuaran–Churumuco, 18°48.8520′N 101°54.9558′W, 248 m, 30.vi.2008, O.F. Francke, H. Montaño, J. Ponce, and A. Quijano, 1♂, 1♀ paratypes (AMNH).

Maaykuyak, gen. nov.
Figures 6, 7, 22B, 26B; table 1

Vejovis vittatus Williams, 1970 [= *Maaykuyak vittatus* (Williams, 1970), comb. nov.], type species, here designated.

Vejovis spinigerus group (part): Gertsch and Soleglad, 1972: 605.

Vaejovis eusthenura group (part): Williams, 1980: 55; Sissom and Francke, 1985: 1; Sissom, 1991: 26; Stockwell, 1992: 408, 409; Sissom, 1993: 68; Lourenço and Sissom, 2000: 135; Sissom, 2000: 530, 532, 551; Armas and Martín-Frías, 2001: 8; McWest, 2009: 8, 48, 52, 56, 61, 64, 98, 101–103, 108, table 1; Ponce-Saavedra and Sissom, 2004: 541; González-Santillán, 2004: 29; Francke and Ponce-Saavedra, 2005: 67; Sissom and Hendrixson, 2005a: 131; 2005b: 33, 34; Fet et al., 2006a: fig. 17, tables 1, 3; 2006b: 8; Graham and Soleglad, 2007: 9, 11, 12; Soleglad et al., 2007: 134, 135; Santibáñez-López and Sissom, 2010: 49.

Hoffmannius (part): Soleglad and Fet, 2008: 1, 26, 57, 60, 89, 91, 96, 102; Ayrey and Soleglad, 2011: 1.

Etymology: *Maaykuyak*, gen. nov., is a noun in apposition, masculine in gender, meaning "god of the warriors" in the language of the Kiliwa people from northern Baja California.

Diagnosis: *Maaykuyak*, gen. nov., can be separated from other genera of Syntropinae by the presence of a medium-sized oval, whitish glandular area on the dorsal medial surface of the telson vesicle in adult males, which is reduced in adult females (fig. 26B). Additional diagnostic characters of the genus are as follows: pedipalp chela manus, dm, dpl, drl, drs, and pld carinae absent (not differing in height or texture from adjacent intercarinal surfaces), dorsal intercarinal surfaces rounded, not concave, and fixed finger trichobothrium *et* situated between RD3 and RD4, closer to RD4; metasomal segments I–V, lateral surfaces glabrous, segment V, dm carina partially infuscated, infuscation not extending full length of segment. *Maaykuyak*, gen. nov., and its sister genus, *Konetontli*, gen. nov., each bear five fully developed retroventral macrosetae on the basitarsus of leg III (fig. 22B), compared with other genera of Syntropinae, which bear at least six.

Maaykuyak waueri, comb. nov., further resembles the species of *Konetontli*, gen. nov., in being one of the smallest species in the subfamily, adults measuring 15–25 mm in total length. However, these genera can be separated by the presence of a subaculear tubercle in *Konetontli*, gen. nov., which is absent in *Maaykuyak*, gen. nov. Species of *Mesomexovis*, gen. nov., resemble *Maaykuyak*, gen. nov., in the pattern of infuscation of the sclerites, but are larger and lack a glandular area on the dorsal median surface of the telson vesicle.

Maaykuyak, gen. nov., shares with *Konetontli*, gen. nov., *Kuarapu*, *Syntropis*, *Vizcaino*, gen. nov., *Chihuahuanus bilineatus*, comb. nov., *C. coahuilae*, comb. nov., and *Thorellius cristimanus* the presence of a secondary hook on the hemispermatophore, created by an extension of the axial carina of the distal lamina, that forms a pronounced bifurcation with the primary hook.

Included Species: *Maaykuyak vittatus* (Williams, 1970), comb. nov.; *Maaykuyak waueri* (Gertsch and Soleglad, 1972), comb. nov.

Distribution: *Maaykuyak*, gen. nov., is endemic to Mexico (recorded from the states of Baja California Sur, Chihuahua, Coahuila, Durango, and Nuevo León) and the United States (recorded only from Texas; fig. 6). This genus has a disjunct distribution: *Maaykuyak vittatus*, comb. nov., occurs in the southern third of the Baja California Peninsula, whereas *Maaykuyak waueri*, comb. nov., inhabits the northern ranges of the Chihuahuan Desert. This distribution suggests that vicariance was promoted initially by the uplift of the Sierra Madre Occidental and subsequently by the separation of the Baja California Peninsula from the North American mainland.

Natural History: *Maaykuyak vittatus*, comb. nov., inhabits subtropical deciduous forest from sea level to 850 m altitude, whereas *M. waueri*, comb. nov., inhabits the Chihuahuan Desert, from 620–1922 m. Although commonly collected at night with UV light detection, both species have also been found during the day, by turning stones and disturbing leaf litter. Both species appear to prefer slightly mesic habitats, e.g., they are more abundant under forest canopy or near oases. The habitat and habitus of *Maaykuyak*, gen. nov., is consistent with the lapidicolous ecomorphotype (Prendini, 2001a).

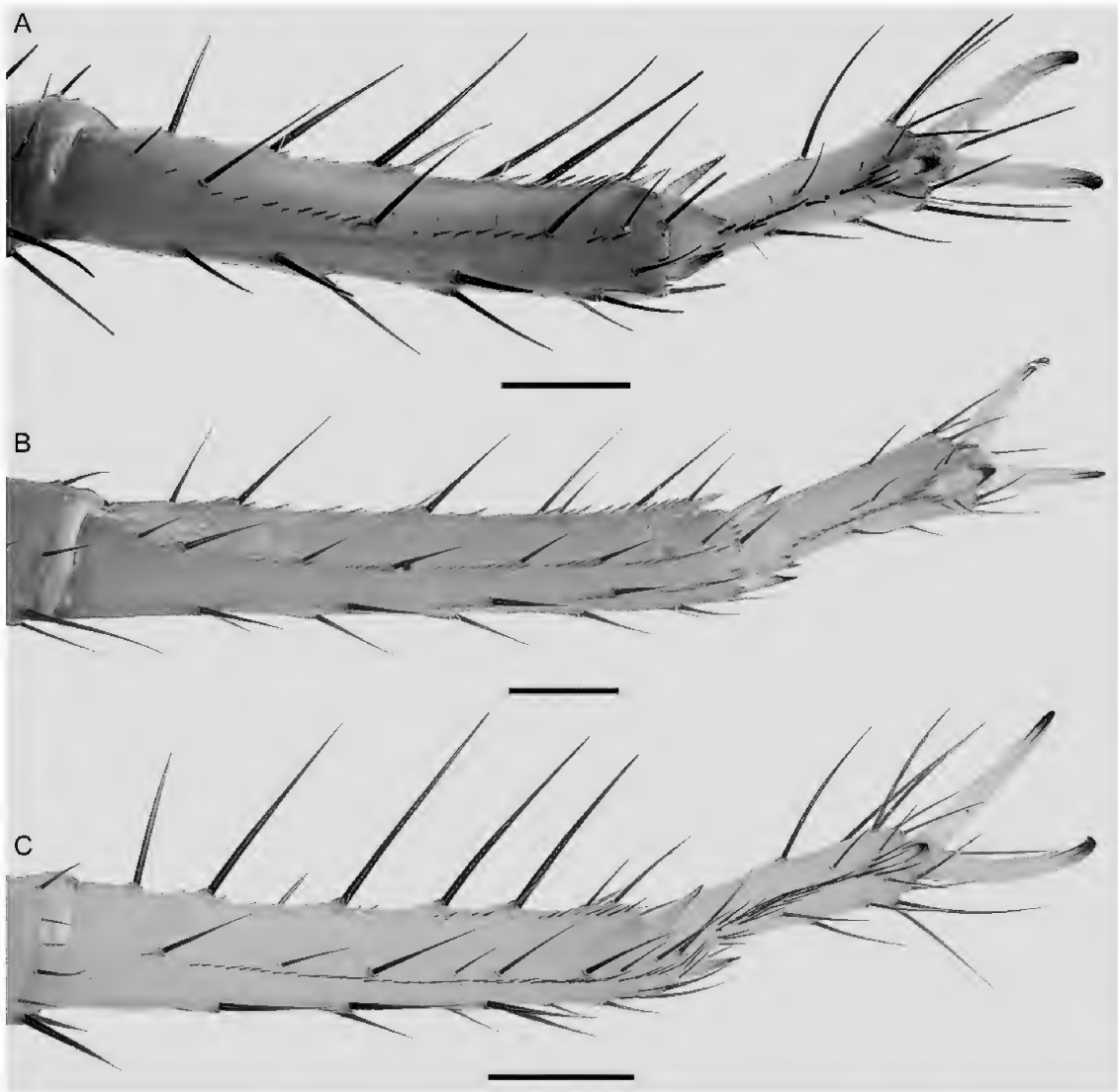


Fig. 21. Syntropinae Kraepelin, 1905, dextral leg III, basitarsus and telotarsus, ventral aspect, illustrating macrosetae and spinules. **A.** *Chihuahuanus globosus* (Borelli, 1915), comb. nov., ♂ (AMNH). **B.** *Thorellius intrepidus* (Thorell, 1876), ♂ (AMNH). **C.** *Vizcaino viscainensis* (Williams, 1970), comb. nov., ♂ (AMNH). Scale bars = 0.5 mm.

REMARKS: Both species of this genus were previously assigned to the *eusthenura* group of *Vaejovis* (Williams, 1980; Sissom, 2000), for which Soleglad and Fet (2008) devised the name *Hoffmannius*, without quantitatively testing its monophyly or composition. *Hoffmannius*, as defined by Soleglad and Fet (2008), was consistently polyphyletic, and the two species hereby assigned to *Maaykuyak*, gen. nov., consistently monophyletic, in the phylogenetic analyses of González-Santillán and Prendini (in press) based on morphology and those based on morphology and DNA. *Maaykuyak*, gen. nov., was not related to the species Soleglad and Fet (2008) assigned to *Hoffmannius*, forming a monophyletic group with *Konetontli*, gen. nov., instead (fig. 7). The creation of a new genus for these species is based on their phylogenetic position and unique, diagnostic character combination.

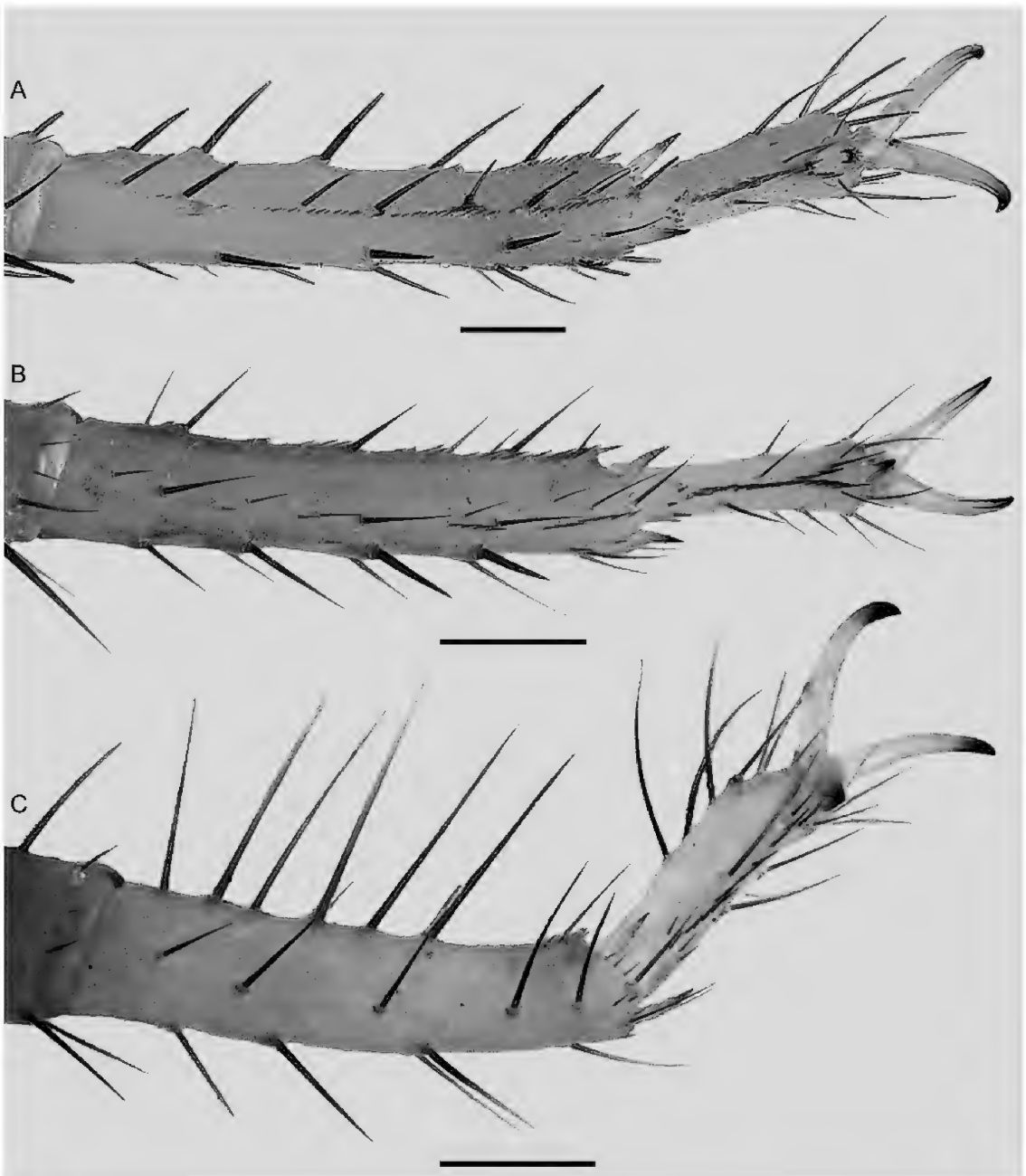


Fig. 22. Syntropinae Kraepelin, 1905, dextral leg III, basitarsus and telotarsus, ventral aspect, illustrating macrosetae and spinules. **A.** *Kochius punctipalpi* (Wood, 1863), ♂ (AMNH). **B.** *Maaykuyak waueri* (Gertsch and Soleglad, 1972), comb. nov., ♂ (AMNH). **C.** *Paravaejovis pumilis* (Williams, 1980), ♂ (AMNH). Scale bars = 0.5 mm.

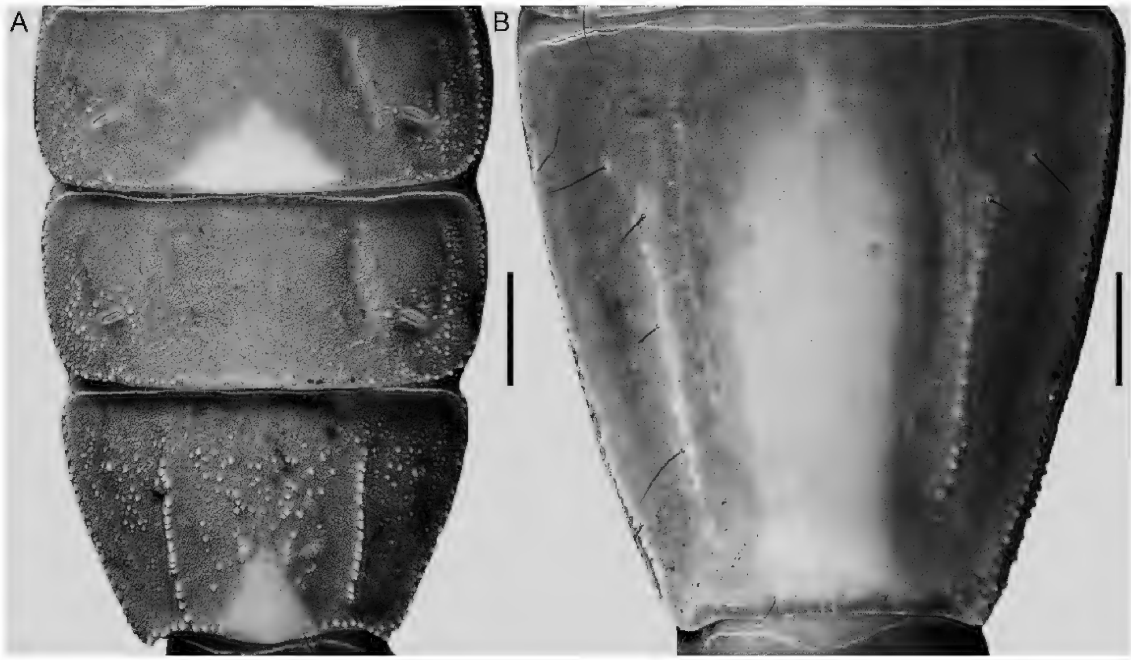


Fig. 23. Syntropinae Kraepelin, 1905, mesosomal sternites, ventral aspect, illustrating glandular areas on ventral surfaces. **A.** *Kochius bruneus* (Williams, 1970), ♂ (AMNH), sternites V–VII. **B.** *Syntropis macrura* Kraepelin, 1900, ♂ (AMNH), sternite VII. Scale bars = 1 mm.

MATERIAL EXAMINED: *Maaykuyak vittatus* (Williams, 1970), comb. nov.: **MEXICO: Baja California Sur:** *Municipio de Comondú*: San Miguel Comondú, 5 mi. SW, 1000 ft, 2.vii.1968, S.C. Williams and M.A. Cazier, holotype ♂ (CAS Type No. 10430); San Miguel Comondú, 8–16 km SW, 304 m, 3.vii.1968, S.C. Williams and M.A. Cazier, 1♂, 1♀ paratypes (AMNH). *Maaykuyak waueri* (Gertsch and Soleglad, 1972), comb. nov.: **MEXICO: Durango:** *Municipio de Tlahualilo*: Hwy 49, at deviation Montes Claros–Tlahualilo de Zaragoza, 26°09.242′N 103°31.284′W, 1107 m, 6.viii.2005, O.F. Francke, W.D. Sissom, K.J. McWest, C. Lee, H. Montaño, J. Ballesteros, L. Jarvis, and C. Durán, 1♂, 1♀ (AMNH). **U.S.A.: Texas:** *Brewster Co.*: Big Bend National Park: The Basin, Chisos Mountains, 28.ix.1950, holotype ♀ (AMNH).

Mesomexovis, gen. nov.
Figures 2D, 6, 7, 19A, B, 27B; table 1

Vejovis punctatus Karsch, 1879 [= *Mesomexovis punctatus* (Karsch, 1879), comb. nov.], type species, here designated.

Vejovis first section (part): Hoffmann, 1931: 134, 139.

Vejovis eusthenura group (part): Williams 1970a: 395, 396.

Vaejovis eusthenura group (part): Williams, 1980: 55; Sissom, 1991: 26; Stockwell, 1992: 408, 409; Sissom, 1993: 68; Lourenço and Sissom, 2000: 135; Sissom, 2000: 530, 534, 535; Armas and Martín-Frías, 2001: 8; González-Santillán, 2004: 29; Ponce-Saavedra and Sissom, 2004: 541; Francke and Ponce-Saavedra, 2005: 67; Sissom and Hendrixson, 2005b: 33, 34; Fet et al., 2006a: 7; 2006b: tables 1, 9; Graham and Soleglad, 2007: 9, 11, 12; Soleglad et al., 2007: 134, 135; McWest, 2009: 8, 48, 52, 56, 61, 64, 98, 101–103, 108 table 1; Santibáñez-López and Sissom, 2010: 49.

Vaejovis intrepidus group (part): Sissom, 1989: 180; 1991: 24, 26; Stockwell, 1992: 409; Sissom, 1993: 68; Lourenço and Sissom, 2000: 135; Sissom, 2000: 537, 538, 551; Armas and Martín-Frías, 2001: 8; Hendrixson 2001: 47; González-Santillán, 2004: 30, 31; Ponce-Saavedra and Sissom, 2004: 539, 541; Graham and Fet, 2006: 7; McWest, 2009: 66, 69, 70, 100–102, table 1; Santibáñez-López and Sissom, 2010: 52.

Vaejovis punctipalpi group (part): Francke and González-Santillán, 2007: 586, 587, 590; Graham and Soleglad, 2007: 11, 12; Soleglad et al., 2007: 134, 135.

Hoffmannius (part): Soleglad and Fet, 2008: 4, 91, tables 3, 5, 9; Ayrey and Soleglad, 2011: 1.
Kochius (part): Soleglad and Fet, 2008: 1, 26, 30, 35, 57, 60, 66, 73, 92–95, 102, tables 4, 9; Ayrey and Soleglad, 2011: 1.
Thorellius (part): Soleglad and Fet, 2008: 1, 5, 30, 35, 53, 67, 73, 94, 95, 102, fig. 26, tables 1, 4, 9; Ayrey and Soleglad, 2011: 1.

ETYMOLOGY: The generic name is a noun in apposition that combines three words, the Greek prefix "meso," meaning "middle," the first three letters of the country name "Mexico" and the last three letters of the genus *Vaejovis*, and is masculine in gender. The name refers to the distribution of the genus, which is endemic to the central states of Mexico, and to the original placement of its component species within the genus *Vaejovis*.

DIAGNOSIS: Species of *Mesomexovis*, gen. nov., are characterized by infuscate carinae on the pedipalp chela, patella, and femur. Infuscation of the chela dpl, plm, vrl, and vrs carinae is complete, extending the entire length of the manus, although ornamentation is absent, i.e., there is no difference in height or texture between these carinae and the adjacent intercarinal surfaces (fig. 19A, B). In contrast, the pedipalp patellar vrl and femoral rlds carinae are smooth and costate in most species of *Mesomexovis*, gen. nov. The vsm and vl carinae of metasomal segments I–IV are also markedly infuscate in most species of the genus, except *M. atenango*, comb. nov., as in some *Chihuahuanus*, gen. nov., and *Paravaejovis* species. However, species of *Chihuahuanus*, gen. nov., may be separated from *Mesomexovis*, gen. nov., by the presence of a small fusiform, whitish glandular area on the dorsal surface of the telson, near the base of the aculeus (fig. 26A), whereas most species of *Paravaejovis* may be separated by the pale and immaculate integument.

Additionally, the vl carinae are smooth and costate (sometimes obsolete), and the vsm carinae obsolete to absent, on sternite VII and metasomal segments I–IV, in most species of *Mesomexovis*, gen. nov. (fig. 27B). The ventral intercarinal surfaces of metasomal segment V are uniformly, finely granular (matte) to shagreened.

Mesomexovis, gen. nov., resembles *Maaykuyak*, gen. nov., in displaying similar patterns of infuscation on the carapace and tergites, as well as glabrous lateral intercarinal surfaces on metasomal segments I–V. The two genera may be separated by the presence of a medium-sized oval, whitish glandular area on the dorsal medial surface of the telson vesicle in *Maaykuyak*, gen. nov. (fig. 26B), which is absent in *Mesomexovis*, gen. nov.

Mesomexovis, gen. nov., shares with *Kuarapu* the completely infuscated rlds and rlm carinae of the pedipalp patella, but differs from *Kuarapu* in the shorter pedipalp chela fingers with relatively proximal trichobothria (fig. 19A, B; cf. fig. 18C, D), and the obsolete to absent vsm carinae of metasomal segments I–IV (fig. 27B; cf. fig. 24B).

INCLUDED SPECIES: *Mesomexovis atenango* (Francke and González-Santillán, 2007), comb. nov.; *Mesomexovis oaxaca* (Santibáñez-López and Sissom, 2010), comb. nov.; *Mesomexovis occidentalis* (Hoffmann, 1931), comb. nov.; *Mesomexovis punctatus* (Karsch, 1879), comb. nov.; *Mesomexovis spadix* (Hoffmann, 1931), comb. et stat. nov.; *Mesomexovis subcristatus* (Pocock, 1898), comb. nov.; *Mesomexovis variegatus* (Pocock, 1898), comb. nov.

DISTRIBUTION: *Mesomexovis*, gen. nov., is endemic to Mexico, and has been recorded from 18 states on the mainland: Aguascalientes, Colima, Chiapas, Guanajuato, Guerrero, Hidalgo, Jalisco, Estado de México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Sinaloa, Querétaro, Tlaxcala, Veracruz, and Zacatecas (fig. 6). The known distribution of this genus encompasses the mountain ranges of the Trans-Mexican Volcanic Belt, the valleys along the Pacific coast, extending from the southern limits of the Sierra Madre Occidental to the Isthmus of Tehuantepec and the Balsas Depression.

NATURAL HISTORY: Species of *Mesomexovis*, gen. nov., occur at the greatest range and the highest altitudes among Syntropinae, from sea level to 2600 m altitude, where they inhabit temperate and tropical deciduous forest and semidesert habitats. These scorpions appear to be maladapted to xeric conditions and are replaced by species of *Chihuahuanus*, gen. nov., and *Paravaejovis* in

the northern part of mainland Mexico and the southwestern United States. Unlike *Chihuahuanus*, gen. nov., and *Paravaejovis*, *Mesomexovis*, gen. nov., exhibits a pronounced seasonal activity. Observations by the first author suggest that species of the genus are active during the rainy season, often becoming the numerically dominant species at particular localities, and estivate during the dry season, when the number of individuals active on the surface dwindles drastically. Due to this phenology, *Mesomexovis*, gen. nov., species are more commonly collected during the rainy season, by turning stones during the day and with UV light detection at night. The habitat and habitus are consistent with the lapidicolous ecomorphotype (Prendini, 2001a).

REMARKS: This genus accommodates species previously assigned to the *eusthenura*, *intrepidus*, and *punctipalpi* groups of *Vaejovis*, first proposed by Hoffmann (1931), Williams (1970a, 1971a), and Sissom (1989). Soleglad and Fet (2008) devised the names *Hoffmannius*, *Thorellius*, and *Kochius* for these groups, respectively, without quantitatively testing their monophyly and composition. All three genera, as defined by Soleglad and Fet (2008), were consistently polyphyletic, and the group of species hereby assigned to *Mesomexovis*, gen. nov., consistently monophyletic, in the phylogenetic analyses of González-Santillán and Prendini (in press) based on DNA and those based on morphology and DNA. *Mesomexovis atenango*, comb. nov., was previously assigned to the *punctipalpi* group (Francke and González-Santillán, 2007) and then to *Kochius* (Soleglad and Fet, 2008); *M. occidentalis*, comb. nov., and *M. subcristatus*, comb. nov., to the *intrepidus* group (Hoffmann, 1931; Sissom, 1989, 2000) and then to *Thorellius* (Soleglad and Fet, 2008); and *M. oaxaca*, comb. nov., to the *eusthenura* group (Santibáñez-López and Sissom, 2010).

González-Santillán and Prendini (in press) identified sufficient, consistent diagnostic character differences to elevate to species rank, *M. spadix*, comb. et stat. nov., formerly recognized as a subspecies of *M. punctatus*, comb. nov., and reinstate to its original rank as species, *M. variegatus*, comb. nov., also formerly considered a subspecies of *M. punctatus*, comb. nov. (Hoffmann, 1931; Sissom, 2000).

MATERIAL EXAMINED: *Mesomexovis atenango* (Francke and González-Santillán, 2007), comb. nov.: **MEXICO: Guerrero:** *Municipio de Copalillo*: Totonimitla, Papalutla, 18°01.4700′N 98°53.8092′W, 650 m, 28.i.2011, U. Lonjino and J. Mendez, 1♂, 1♀ (IBUNAM). *Municipio de Tepecoacuilco de Trujano*: Cerro de la Coronilla, 18°0.9756′N 99°31.7256′W, 844 m, 27.vi.2008, O.F. Francke, A. Quijano, and C. Santibáñez, 1♂, 1♀ (IBUNAM); Cerro de la Coronilla, 3.4 km NE of Ahuehuepan, 18°00′57″N 99°31′32″W, 857 m, 23–24.x.2009, A. Valdez, T. López, and C. Quijano, 1♂, 1♀ (IBUNAM). *Mesomexovis spadix* (Hoffmann, 1931), comb. et stat. nov.: **MEXICO: Guanajuato:** *Municipio de León*: León, iv.2004, P. Berea, 1♂, 1♀ (IBUNAM). *Mesomexovis oaxaca* (Santibáñez-López and Sissom, 2010), comb. nov.: **MEXICO: Oaxaca:** *Municipio de Ocotlán*: Chichicapan, 4.8 km E, 1645 m, 23.viii.1966, C.M. Bogert, 1♂, 1♀ (AMNH). *Municipio de San Pablo Villa Mitla*: Mitla, 8 km NE, on ridge ca. 6800–7200 ft, near El Crucero ruins, 27.viii.1963, C.M. Bogert, G. Sluder, and N. Bucknall, 1♂, 1♀ (AMNH). *Municipio de Tlacolula de Matamoros*: Tlacolula, 16.vii.1955, C. and P. Wauer, 1♂, 1♀ paratypes (AMNH). *Mesomexovis occidentalis* (Hoffmann, 1931), comb. nov.: **MEXICO: Guerrero:** *Municipio de Acapulco*: Acapulco, holotype ♀ of *Vaejovis subcristatus occidentalis* Hoffmann, 1931 (AMNH), H. Hoffmann, 1♂, 1♀ paratypes (AMNH); Cumbres de Llano Largo, 16°49.505′N 99°49.999′W, 371 m, 19.vi.2007, O.F. Francke, H. Montaño, and A. Ballesteros, 1♂ (CAS [ARA 1975]). *Municipio de Copala*: Microwave antenna Fogos, E of Copala, 16°33.9918′N 98°53.30′W, 103 m, 22.vi.2007, O.F. Francke, H. Montaño, L. Escalante, and A. Ballesteros, 1♂, 1♀ (IBUNAM). *Mesomexovis punctatus* (Karsch, 1879), comb. nov.: **MEXICO: Hidalgo:** *Municipio de Zimapán*: Microwave antenna at Zimapán, 20°44.7828′N 99°20.8998′W, 1900 m, 3.viii.2002, L. Prendini, O.F. Francke, E. González, and J. Ponce, 2♂, 2♀ (AMNH [ARA 1170]). *Mesomexovis subcristatus* (Pocock, 1898), comb. nov.: **MEXICO: Oaxaca:** *Municipio de Cuicatlán*: Tomellin, 17°45.180′N 96°57.237′W, 605 m, 23.vii.2002, L. Prendini, O.F. Francke, E. González, and J. Ponce, 1♂, 1♀ (AMNH [LP

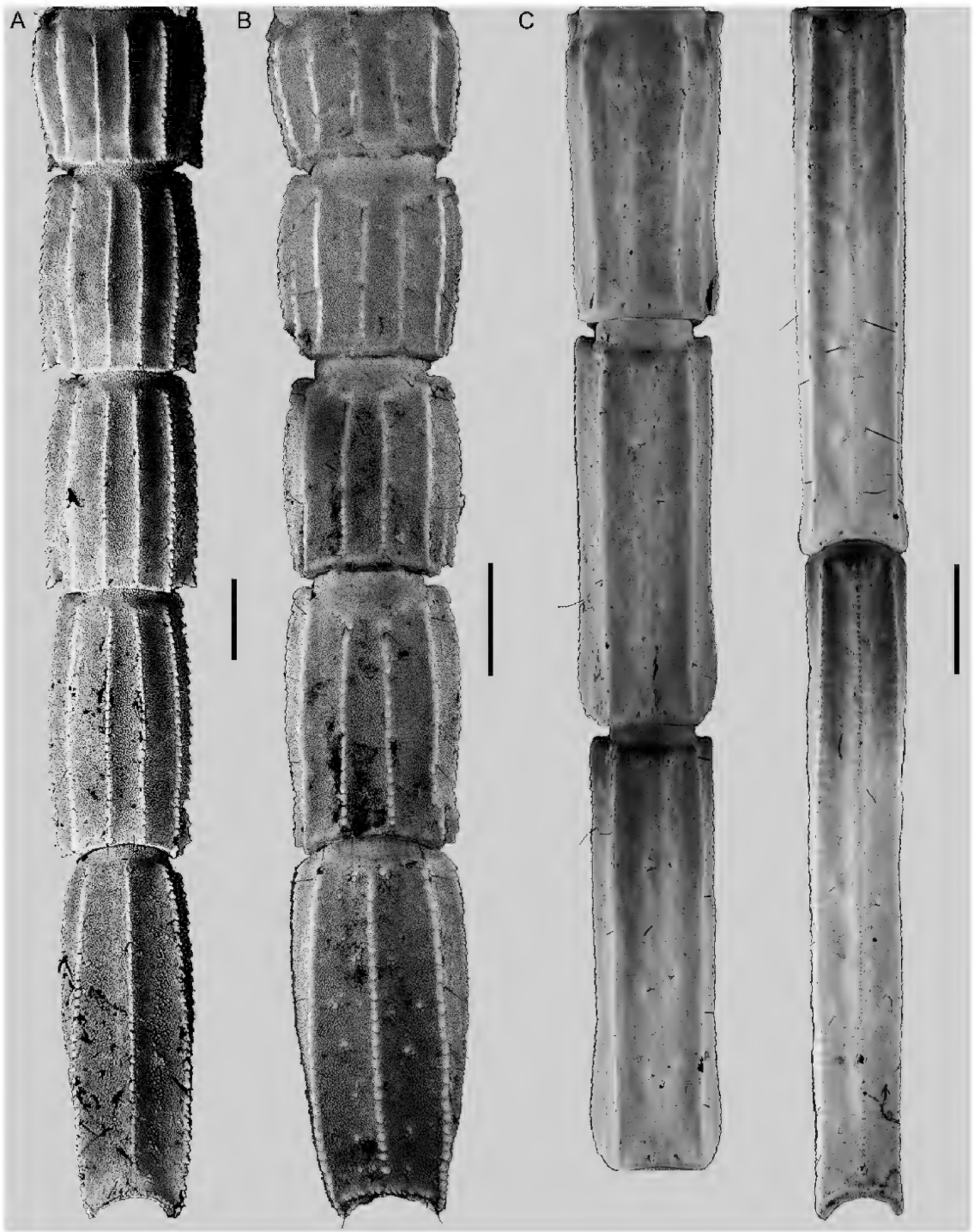


Fig. 24. Syntropinae Kraepelin, 1905, metasomal segments I–V, ventral aspect, illustrating carinae. **A.** *Kochius bruneus* (Williams, 1970), ♂ (AMNH). **B.** *Kuarapu purhepecha* Francke and Ponce-Saavedra, 2010, paratype ♂ (AMNH). **C.** *Syntropis macrura* Kraepelin, 1900, ♂ (AMNH). Scale bars = 1 mm (**A, B**), 2.5 mm (**C**).

2086]). **Puebla:** *Municipio de Tehuacán*: Tehuacán, 2 km E, 18°24.002′N 97°22.867′W, 1435 m, 25.vii.2002, L. Prendini, O.F. Francke, E. González, and J. Ponce, 1♂, 1♀ (AMNH [LP 2048]). *Mesomexovis variegatus* (Pocock, 1898), comb. nov.: **MEXICO: Guerrero:** *Municipio de Buenavista de Cuellar*: El Comal, 18°27.086′N 99°17.139′W, 1749 m, 13.vi.2007, O.F. Francke et al., 1♂, 1♀ (AMNH [ARA 2623]).

Paravaejovis Williams, 1980
Figures 1C, 2C, E, 3, 7, 19C, D, 22C, 27C, 28C; table 1

Vejovis pumilis Williams, 1970 [= *Paravaejovis pumilis* (Williams, 1980)], type species, by monotypy.

Vejovis first section (part): Hoffmann, 1931: 134, 139.

Vejovis eusthenura group (part): Williams, 1970a: 395, 396.

Vejovis pumilis group: Williams, 1970b: 297, figs. 13, 14.

Vaejovis eusthenura group (part): Williams, 1980: 55; Sissom and Francke, 1985: 1; Sissom, 1991: 26; Stockwell, 1992: 408, 409; Sissom, 1993: 68; Lourenço and Sissom, 2000: 135; Sissom, 2000: 530, 532, 551; Armas and Martín-Frías, 2001: 8; McWest, 2009: 8, 48, 52, 56, 61, 64, 98, 101–103, 108, table 1; González-Santillán, 2004: 29; Ponce-Saavedra and Sissom, 2004: 541; Francke and Ponce-Saavedra, 2005: 67; Sissom and Hendrixson, 2005a: 131; 2005b: 33, 34; Fet et al., 2006a: 7; 2006b: tables 1, 9; Graham and Soleglad, 2007: 9, 11, 12; Soleglad et al., 2007: 134, 135; Santibáñez-López and Sissom, 2010: 49.

Paravaejovis Williams, 1980: 29, 30, fig. 32A–D; Haradon, 1984b: 319; Francke, 1985: 11, 21; Sissom, 1990: 107, 110, 114, 106, fig. 3.19A; Nenilin and Fet, 1992: 9; Stockwell, 1992: 409, 416, figs. 62, 63; Fet et al., 1998: 617; Kovařík, 1998: 143; Beutelspacher, 2000: 56, 63, 151; Sissom, 2000: 504, 505; Soleglad and Fet, 2003: 88; 2005: 5, 6; Prendini and Wheeler, 2005: 482, table 10; Fet et al., 2006a: 4, 7, 9, 13, fig. 6, tables 1, 2,; 2006b: 1, 2, 4, 5, 7, 8, figs. 5, 6, tables 1, 2; 2006c: 1, 2, 4, 5, 8, figs. 5, 6, table 1; Soleglad and Fet, 2006: 5, 6, 10, 12, 13, 26, tables 2, 3; 2008: 1, 3, 5, 6, 12, 13, 24, 25, 28, 30, 34, 35, 37, 38, 40, 43, 51, 54, 55, 60, 62, 63, 70, 71, 73, 76–78, 82–84, 102, figs. 1, 7, 18, 19, 57, 97–99, 126, 163, 189, 191, 196, 197, 201, tables 1, 2, 7, 8, 9; Dupré, 2007: 9, 16, 17.

Lissovaejovis Ponce-Saavedra and Beutelspacher, 2001, syn. nov.: 88 [nomen nudum].

Hoffmannius Soleglad and Fet, 2008, syn. nov.: 1, 4, 26, 57, 60, 89, 91, 96, 102; *Buthus eusthenura* Wood, 1863 [= *Paravaejovis eusthenura* (Wood, 1863), comb. nov.], type species, by original designation; Ayrey and Soleglad, 2011: 1.

DIAGNOSIS: Species of *Paravaejovis* may be separated from other genera of Syntropinae by the following combination of characters. The pedipalp chela manus drl carina and the patellar rlds and rlm carinae are usually complete and smooth, costate (fig. 19C, D), becoming obsolete in some species, e.g., *P. pumilis*. Pedipalp chela trichobothrium *esb* is situated between RD5 and RD6, and/or their associated macrosetae, and trichobothrium Et_5 at the base of the fixed finger, distal to the movable finger articulation and removed from Et_4 (fig. 19D), the exception being *P. pumilis*, in which *esb* is situated at the position of RD6 (only the associated macroseta is present) and Et_5 is situated at the base of the fixed finger, proximal to the movable finger articulation but slightly distal to Et_4. The median denticle row on the pedipalp chela fixed finger comprises six primary subrows of median denticles, separated by six retrolateral denticles (fig. 19C, D) in all *Paravaejovis* species except *P. pumilis*, *P. puritanus*, comb. nov., and *P. schwenkmeyeri*, comb. nov., in which it comprises five primary subrows of median denticles, separated by five retrolateral denticles.

Paravaejovis are most closely related to *Chihuahuanus*, gen. nov., and *Mesomexovis*, gen. nov. However, compared with *Chihuahuanus*, gen. nov., and *Mesomexovis*, gen. nov., which exhibit an incrassate chela manus and relatively short fingers, most species of *Paravaejovis* exhibit a slender chela manus and elongate fingers, the exceptions being *P. gravicaudus*, comb. nov., *P. pumilis*, and *P. spinigerus*, comb. nov., in which the manus is more incrassate. Most species of *Paravaejovis* present psammophilous adaptations that are absent in *Mesomexovis*, gen. nov., and most species of *Chihuahuanus*, gen. nov.: pale, immaculate coloration, glabrous integument, and numerous long macrosetae on the legs, with the dorsal and retrodorsal macrosetae on the basitarsi of legs I–III arranged in a single row (setal combs) (fig. 22C). *Chihuahuanus globosus*, comb. nov., exhibits such characters but may be separated from *Para-*

vaejovis by the presence of a small fusiform, whitish glandular area anterior to the base of the aculeus on the dorsal surface of the telson vesicle (as illustrated for *C. coahuilae*, comb. nov., in fig. 26A). In addition, the vl carinae of metasomal segments I–IV are usually granular in *Chihuahuanus*, gen. nov. (fig. 27A), but smooth in many species of *Paravaejovis* (fig. 27C), exceptions being *P. confusus*, comb. nov., *P. waeringi*, comb. nov., and *P. pumilis* (fig. 28C). Although there are notable exceptions (e.g., *P. spinigerus*, comb. nov.), most species of *Paravaejovis* differ from *Mesomexovis*, gen. nov., in the pale, immaculate integument of the carapace and mesosomal tergites, which are markedly infuscated in the latter.

INCLUDED SPECIES: *Paravaejovis confusus* (Stahnke, 1940), comb. nov.; *Paravaejovis diazi* (Williams, 1970), comb. nov.; *Paravaejovis eusthenura* (Wood, 1863), comb. nov.; *Paravaejovis flavus* Banks, 1900, comb. nov.; *Paravaejovis galbus* (Williams, 1970), comb. nov.; *Paravaejovis gravicaudus* (Williams, 1970), comb. nov.; *Paravaejovis hoffmanni* (Williams, 1970), comb. nov.; *Paravaejovis pumilis* (Williams, 1970); *Paravaejovis puritanus* (Gertsch, 1958), comb. nov.; *Paravaejovis schwenkmeyeri* (Williams, 1970), comb. nov.; *Paravaejovis spinigerus* (Wood, 1863), comb. nov.; *Paravaejovis waeringi* (Williams, 1970), comb. nov.

DISTRIBUTION: *Paravaejovis* is endemic to Mexico (recorded from Baja California, Baja California Sur, Chihuahua, Sinaloa, and Sonora) and the United States (recorded from Arizona, California, Nevada, New Mexico, Oregon, and Utah; fig. 3). All except three of the 12 currently recognized species (*P. confusus*, comb. nov.; *P. spinigerus*, comb. nov.; *P. waeringi*, comb. nov.), occurring in the Great Basin, Mojave, and Sonoran (including Colorado) deserts on the North American mainland, are endemic to the Baja California Peninsula, having diversified in isolation from their mainland relatives after the opening of the Gulf of California. This genus is absent from the Chihuahuan Desert.

NATURAL HISTORY: Most species of this genus are fossorial inhabitants of desert and semidesert regions, more commonly collected by UV light detection at night than under stones or other debris during the day. Species inhabiting the Baja California Peninsula have been collected from sea level to 1180 m altitude, those on the North American mainland mostly above 2000 m. Sandy substrata evidently played an important role in the diversification of *Paravaejovis* in Baja California. Most species on the peninsula are psammophilous or ultrapsammophilous, characterized by pale coloration, the absence of infuscation, a smooth, glabrous integument, and setal combs on the leg tarsi, for burrowing in sand (Fet et al., 1998; Prendini, 2001a). The mainland species, by contrast, appear to be less specialized and inhabit a greater range of substrata, from sand dunes to rock walls, and vegetation types, from desert to pine-oak forest which, although present on the peninsula, is uninhabited by *Paravaejovis*.

Paravaejovis pumilis from Baja California Sur evolved such specialized ultrapsammophilous adaptations that it was long thought related to the largely psammophilous subfamily Smeringurinae Soleglad and Fet, 2008, and to the *borregoensis* microgroup of *Paruroctonus* in particular, with which it was suggested to be subordinate (Haradon, 1984b; Sissom, 1990, 2000; Stockwell, 1989, 1992). The *borregoensis* microgroup comprises small psammophilous vaejovids characterized by the absence of a mid-retrosuperior (mrs) macroseta (part of the retroventral series in the terminology used in the present contribution) on the basitarsus of leg II, also observed in *P. pumilis*, which shares with the *borregoensis* microgroup several other characters, some sexually dimorphic, concerning the carapace, pectines, legs, and metasoma (Haradon, 1984b). The putative relationship of *P. pumilis* to *Paruroctonus* and other Smeringurinae, further elaborated by Soleglad and Fet (2003, 2008), was falsified by González-Santillán and Prendini (in press), who demonstrated that it forms a divergent sister species of *P. eusthenura*, comb. nov., *P. diazi*, comb. nov., and *P. hoffmanni*, comb. nov. (fig. 7), separated from the latter and other members of the genus by a series of apomorphic character states, mostly associated with psammophily. Psammophily in *P. pumilis* and other *Paravaejovis* species evolved independently from that in Smeringurinae.

REMARKS: As redefined here, *Paravaejovis* accommodates species mostly assigned to Hoffmann's (1931) "first section" of *Vaejovis*, and then Williams' (1970a) *eusthenura* group, for which Soleglad and Fet (2008) devised the name *Hoffmannius*, without quantitatively testing its monophyly or composition. *Hoffmannius*, as defined by Soleglad and Fet (2008), was consistently polyphyletic, and the group of species hereby assigned to *Paravaejovis* consistently monophyletic, in the phylogenetic analyses of González-Santillán and Prendini (in press) based on DNA and those based on morphology and DNA. The following species are therefore transferred to other genera in the present contribution: *Chihuahuanus bilineatus*, comb. nov., *Chihuahuanus coahuilae*, comb. nov., *Chihuahuanus glabrimanus*, comb. nov., *Chihuahuanus globosus*, comb. nov., *Mesomexovis punctatus*, comb. nov., *Mesomexovis spadix*, comb. nov. et stat., *Mesomexovis variegatus*, comb. nov., *Maaykuyak vittatus*, comb. nov., *Maaykuyak waueri*, comb. nov., and *Vizcaino viscainensis*, comb. nov., previously assigned to the *eusthenura* group (Williams, 1980; Sissom, 2000) and then to *Hoffmannius* (Soleglad and Fet, 2008); and *Mesomexovis oaxaca*, comb. nov., previously assigned to the *eusthenura* group (Santibáñez-López and Sissom, 2010).

In addition, *P. pumilis* was consistently retrieved, in the phylogenetic analyses of González-Santillán and Prendini (in press) based on DNA and those based on morphology and DNA, as the sister species of *P. eusthenura*, comb. nov., the type species of *Hoffmannius*, nested within a larger monophyletic group comprising the remaining species of *Hoffmannius*. *Paravaejovis pumilis* was never recovered close to *Smeringurus grandis* (Williams, 1970), the exemplar species for Smeringurinae, to which it was alleged to belong (Soleglad and Fet, 2008). Among several psammophilous character states, shared with other species of *Paravaejovis* including *P. eusthenura*, comb. nov., *P. pumilis* shares the diagnostic synapomorphy of Syntropinae, i.e., the spinose distal barb margin of the sclerotized hemimating plug on the hemispermatophore, noted but disregarded by Stockwell (1989, 1992) and Soleglad and Fet (2008). The other putatively diagnostic difference, on which basis *P. pumilis* was differentiated from other vaejovids, is the neotrichobothriotaxic pedipalp chela (Williams, 1980). Aside from the fact that neobothriotaxy, as expressed in *P. pumilis*, is autapomorphic and thus uninformative about its phylogenetic placement, "deviations" from the typical "Type C" trichobothrial pattern are not uncommon among Vaejovidae (Haradon, 1984b), occurring, e.g., in three other, unrelated vaejovid taxa (Gertsch and Soleglad, 1972; Sissom and Francke, 1985; Sissom, 1991; Haradon, 1984b; Soleglad and Fet, 2003, 2008): *Franckeus*, *Paruroctonus ammonastes* Haradon, 1984, and *Pseudouroctonus bogerti* (Gertsch and Soleglad, 1972). Such changes may result from simple genetic processes like differential expression of chromosomes and homeotic genes (Scott and Weiner, 1984). Contrary to the prevailing dogma in scorpion systematics, trichobothria should not be given "more evolutionary or taxonomic significance" (Soleglad and Fet, 2008: 84) than other characters. Trichobothria are characters like any other.

In view of the unambiguous phylogenetic position of the type species of *Paravaejovis*, *Hoffmannius* Soleglad and Fet, 2008, is hereby abolished: *Hoffmannius* Soleglad and Fet, 2008 = *Paravaejovis* Williams, 1980, syn. nov. Ten species listed above, formerly placed in *Hoffmannius*, are transferred to *Paravaejovis*.

González-Santillán and Prendini (in press) also identified sufficient, consistent diagnostic character differences to remove *P. schwenkmeyeri*, comb. nov., from synonymy with *P. puritanus*, comb. nov. However, *Vaejovis coloradensis* Williams, 1970, was not found to differ consistently from its senior synonym, *P. waeringi*, comb. nov., with which it is retained in synonymy, following Williams (1980). Two subspecies were not found to differ consistently from the nominotypical forms, with which they are hereby synonymized: *Vaejovis diazi transmontanus* Williams, 1970 = *Paravaejovis diazi* (Williams, 1970), syn. nov.; *Vaejovis hoffmanni fuscus* Williams, 1970 = *Paravaejovis hoffmanni* (Williams, 1970), syn. nov.

The identity of one species assigned to this genus, *P. flavus*, comb. nov., has been problematic since its description. *Vaejovis flavus* Banks, 1900, was briefly described in a key couplet. Soleglad (1973) redescribed the species based on a specimen from the Museum of Comparative Zoology (MCZ), Harvard University, presumed to be the holotype, but which turned out not to be (Sissom, 2000). The holotype was apparently deposited in the U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), the MCZ specimens belong to an undescribed species in the former *punctipalpi* group, and the USNM specimen to the former *eusthenura* group (Sissom, 2000). The type locality of this species is Albuquerque, New Mexico. Several attempts to collect new material matching the description, from the vicinity of the type locality and elsewhere in New Mexico have been unsuccessful (Sissom, 2000), as have attempts to locate the holotype in the USNM. Due to the uncertainty regarding the identity of *P. flavus*, comb. nov., it is considered a nomen dubium pending further investigation.

MATERIAL EXAMINED: *Paravaejovis confusus* (Stahnke, 1940), comb. nov.: **U.S.A.: Arizona:** *Maricopa Co.*: Wickenburg, 20.iv.1938, A.L. Corbin, 2♀ syntypes (CAS Type No. 105170). *Mohave Co.*: Warm Springs Wash, 4.7 km N Topock, 34°44.8662′N 114°28.8996′W, 147 m, 9.ix.2007, L. Prendini and J. Huff, 5♂, 2♀ (AMNH [ARA 3117]). *Paravaejovis diazi* (Williams, 1970), comb. nov.: **MEXICO: Baja California Sur:** *Municipio de Comondú*: Ciudad Constitución, 34.4 km W (= El Crucero, 21.4 mi. W), Magdalena Plain, 75 ft, 26.vii.1968, S.C. Williams and M.A. Cazier, holotype ♂ (CAS Type No. 10413); Punta San Telmo on Gulf coast, 25 ft, 26.v.1969, S.C. Williams, holotype ♂ of *V. diazi transmontanus* (CAS Type No. 10414). *Municipio de La Paz*: Las Cruces, 8 km SW, 30.vii.1968, S.C. Williams and M.A. Cazier, 1♂, 1♀ paratypes (AMNH). *Paravaejovis eusthenura* (Wood, 1863), comb. nov.: **MEXICO: Baja California Sur:** *Municipio de Los Cabos*: San José del Cabo, ca. 10 km S off Route 1, 23°1.7622′N 109°43.49′W, 50 m, 10.vii.2005, W.E. Savary, E. González, and R. Mercurio, 1♂, 1♀ (AMNH [ARA 3177]). *Municipio de La Paz*: La Paz, 18 km SE, 24°2.7498′N 110°8.85′W, 626 m, 8.vii.2004, O.F. Francke, E. González, and A. Valdez, 1♂, 1♀ (AMNH [ARA 1192]). *Paravaejovis galbus* (Williams, 1970), comb. nov.: **MEXICO: Baja California Sur:** *Municipio de Loreto*: Loreto, 8 km S, 16.v.1969, S.C. Williams, holotype ♂ (CAS Type No. 10415), 1♀ allotype, 1♂, 1♀ paratypes (CAS). *Paravaejovis gravicaudus* (Williams, 1970), comb. nov.: **MEXICO: Baja California Sur:** *Municipio de La Paz*: Los Aripes, 21.4 mi. W, 900 ft, 25.vii.1968, S.C. Williams, J. Bigelow, and M. Bentzien, holotype ♂ (CAS Type No. 10418). *Municipio de Comondú*: San Miguel de Comondú, 2 km SW, 3.vii.1968, M.A. Cazier et al., 1♂, 1♀ paratypes (AMNH). *Paravaejovis hoffmanni* (Williams, 1970), comb. nov.: **MEXICO: Baja California Sur:** *Municipio de Comondú*: San Jose de Comondú, 24 mi. NE, 900 ft, 15.v.1969, S.C. Williams, holotype ♂ of *V. hoffmanni fuscus* (CAS Type No. 10421). **Baja California:** *Municipio de Ensenada*: Laguna Manuela, 4.8 km N, 152 m, 22.vi.1968, S.C. Williams and M.A. Cazier, 1♂, 1♀ paratypes (AMNH); Manuela, 3 mi. N, 500 ft, 22.vi.1968, S.C. Williams and M.A. Cazier, holotype ♂ (CAS Type No. 10420). *Paravaejovis pumilis* (Williams, 1970): **MEXICO: Baja California Sur:** Ciudad Constitución (= El Crucero), 26.8 mi. W, Magdalena Plain, 50 m, 26.vii.1968, S.C. Williams and M.A. Cazier, holotype ♂ (CAS Type No. 10425). *Municipio de Comondú*: El Cayuco Fish camp, sand dunes, 24°34.6656′N 111°40.6326′W, 6 m, 11.vii.2005, W.E. Savary, E. González, L. Prendini, and R. Mercurio, 2♂, 2♀ (AMNH [ARA 3173]). *Paravaejovis puritanus* (Gertsch, 1958), comb. nov.: **MEXICO: Baja California:** *Municipio de Ensenada*: Santo Tomas, 8.vii.1953, W.J. and J.W. Gertsch, holotype ♂ (AMNH). **Baja California Sur:** Rancho Canipolé, 1 mi. SW, 800 ft, 15.v.1969, S.C. Williams, holotype ♂ of *Vaejovis terradomus* Williams, 1970 (CAS Type No. 10428). *Paravaejovis schwenkmeyeri* (Williams, 1970), comb. nov.: **MEXICO: Baja California:** *Municipio de Ensenada*: Bahia de Los Angeles, 25 ft, 19.vi.1968, S.C. Williams and M.A. Cazier, holotype ♂ (CAS Type No. 10426). **Baja California Sur:** *Municipio de*

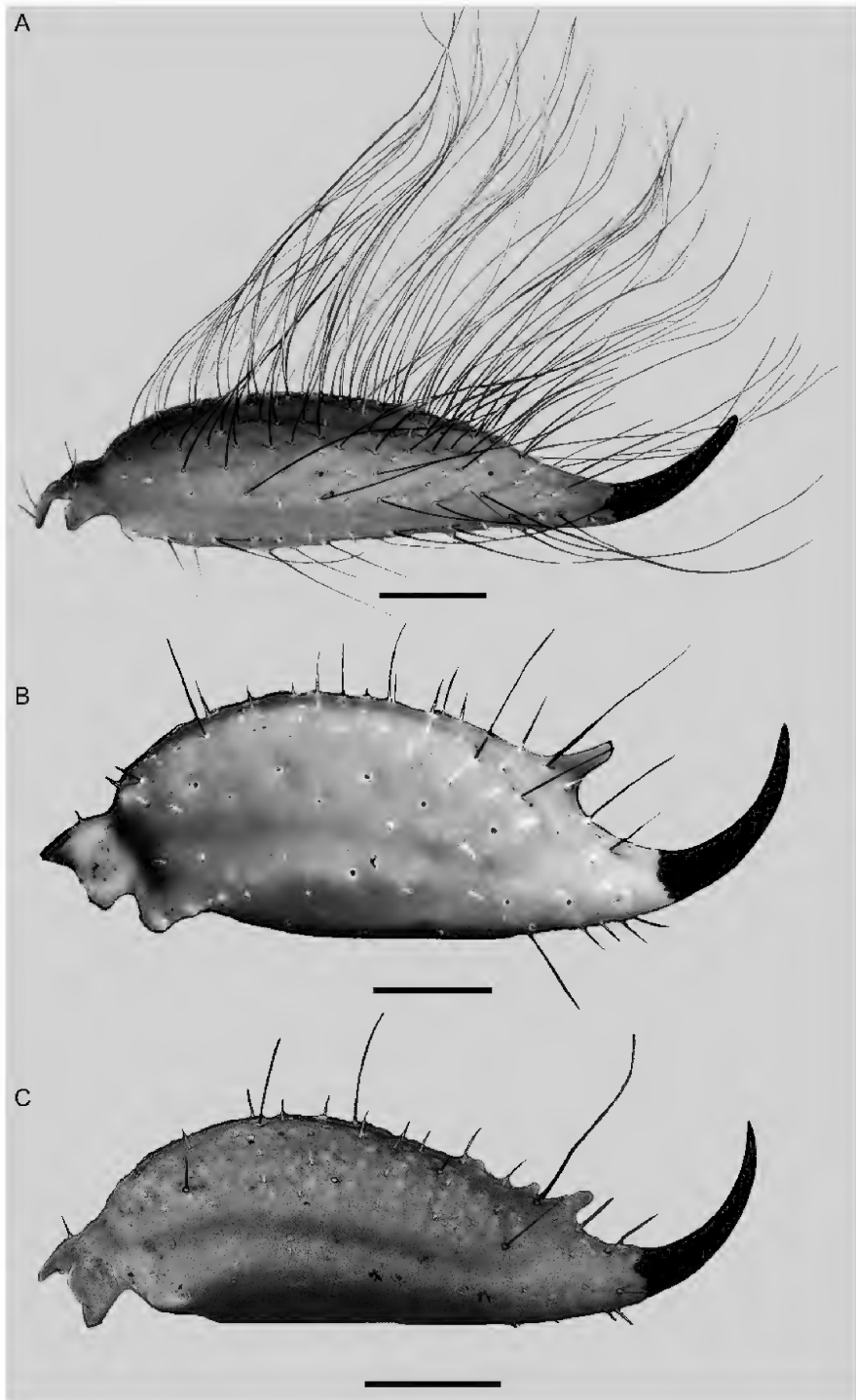


Fig. 25. Syntropinae Kraepelin, 1905, telson, lateral aspect, illustrating macrosetae and subaculear tubercles. **A.** *Kochius hirsuticauda* (Banks, 1910), ♂ (AMNH). **B.** *Konetontli acapulco* (Armas and Martín-Frías, 2004), comb. nov., holotype ♂ (IBUNAM). **C.** *Konetontli nayarit* (Armas and Martín-Frías, 2004), comb. nov., holotype ♂ (IBUNAM). Scale bars = 0.5 mm.

Ensenada: San Raymundo, 12.9 km NW, 152 m, 30.vi.1968, M.A. Cazier et al., 1♂, 1♀ (AMNH). *Paravaejovis spinigerus* (Wood, 1863), comb. nov.: **U.S.A.: Arizona:** *Maricopa Co.*: Sunflower, turnoff to Bushnell Tanks, 33°52′08.8″N 111°27′54.4″W, 1057 m, 6.iv. 2007, J. Huff and L. Prendini, 1♂, 1♀ (AMNH). *Paravaejovis waeringi* (Williams, 1970), comb. nov.: **MEXICO: Baja California:** *Municipio de Ensenada*: Oakies Landing, 27 mi. S of Puertocitos, 12.vi.1968, S.C. Williams and M.A. Cazier, holotype ♂ (CAS Type No. 10431), allotype ♀ (CAS); Puertocitos, 11.vi.1968, S.C. Williams and M.A. Cazier, 2♂, 1♀ (CAS); Puertocitos, 44 km S, Oakies Landing, 12.vi.1968, S.C. Williams and M.A. Cazier, paratype ♂ (AMNH). **U.S.A.: California:** *Imperial Co.*: Algodones Dunes, along Grays Wells Road, S of Interstate Hwy 8, W of Imperial Sand Dunes Recreation Area, 32°44.1756′N 114°53.43′W, 50 m, 31.viii.2005, R. Mercurio and L. Prendini, 1♀ (AMNH [ARA 1499]); Andrade, 2 mi. W, 6.vii.1969, S.C. Williams and V.F. Lee, holotype ♂ (CAS Type No. 10411); *San Diego Co.*: Anza-Borrego Desert State Park: Culp Valley Camp, 33°13.4118′N 116°27.26′W, 1033 m, 30.viii. 2005, R. Mercurio and L. Prendini, 1♂, 1♀ (AMNH [ARA 1497]).

Syntropis Kraepelin, 1900

Figures 1D, 2F, 4, 7, 8A–F, 12–14, 23B, 24C; table 1

Syntropis macrura Kraepelin, 1900, type species, by original designation.

Syntropis Kraepelin, 1900: 16, 17; Birula, 1917a: 163; Werner, 1934: 281; Kästner, 1941: 272; Mello-Leitão, 1945: 118; Stahnke, 1965: 257, 258; Williams, 1969: 285; 1974: 15 (part); Stahnke, 1974: 113–120; Vachon, 1974: 914, 916; Díaz Nájera, 1975: 3, 6; Williams, 1980: 47; Francke, 1985: 13, 18, 20; Sissom, 1990: 110, 114; 1991b: 26; Williams and Savary, 1991: 284; Nenilin and Fet, 1992: 9; Stockwell, 1992: 408; Kovařík, 1998: 146; Beutelspacher, 2000: 55, 70, 152, plate IId; Sissom, 2000: 526; Ponce-Saavedra and Beutelspacher, 2001: 20; Soleglad and Fet, 2003: 15, 36, 67, 144, 163, figs. 66, 79, 80, D-4, tables 3, 4, 9; Fet and Soleglad, 2005: 4, 6, 7; Prendini and Wheeler, 2005: 482, table 10; Soleglad and Fet, 2005: 4, 7; Soleglad et al., 2007: 119–136, figs. 1–37, tables I, II; Soleglad and Fet, 2008: 1, 4, 13, 27, 30, 32, 38, 46, 51, 69, 71–74, 82, 84, 85, 89–92, 95, 104, figs. 10, 27, 53, 82, 106, 110, 139, 151, 180, 203, tables 1–3, 9.

DIAGNOSIS: *Syntropis* differs from other Syntropinae in the carination of metasomal segments I–IV, where the vsm carinae are absent (indicated by pairs of macrosetae only, no difference in ornamentation evident from the adjacent intercarinal surfaces), and the vm carinae distinct (protruding above the adjacent intercarinal surfaces), smooth to finely granular, and unpigmented (fig. 24C). Additional characters that separate *Syntropis* from other genera in the subfamily are as follows. The pedipalps, legs, and metasoma are greatly elongated and slender in adult male *Syntropis*, although less so in females and immatures. *Syntropis* is the only genus in the subfamily that consistently exhibits eight prolateral denticles on the movable finger of the pedipalp chela (fig. 12B). Although *Balsateres* and some *Thorellius* species occasionally exhibit eight prolateral denticles, the basal prolateral denticle is situated adjacent to the preceding prolateral denticle, and up to three adjacent prolateral denticles are often observed (fig. 20A, B), compared with *Syntropis*, in which the prolateral denticles are separate. Adult male *Syntropis* display a whitish glandular area between the vsm carinae of mesosomal sternite VII, extending almost the entire length of the segment (fig. 23B), that is reduced but still evident in females. The dl and lm carinae of metasomal segments I–IV do not project posterolaterally in *Syntropis*, and the terminal granules of these carinae are not noticeably larger than the preceding granules, unlike most genera in the subfamily. Macrosetal counts on the leg basitarsi (23–28) and telotarsi (19–22) of *Syntropis* are greater than those on the basitarsi (14–27 in *Chihuahuanus*, gen. nov., and 16–21 in *Kochius*) and telotarsi (14–17 in *Chihuahuanus*, gen. nov., and 15–18 in *Kochius*) of other genera in the subfamily. *Syntropis* shares with *Kuarapu*, *Vizcaino*, gen. nov., and some species of *Paravaejovis* elongated pedipalp chela fingers and distally displaced trichobothria on the fixed finger, as a consequence of this elongation. However, the positions of trichobothria *ib* and *it* on the fixed finger, with respect to the prolateral denticles, differ among these genera as

Fig. 26. Syntropinae Kraepelin, 1905, telson, dorsal aspect illustrating glandular areas on dorsal surface (demarcated by dotted lines). **A.** *Chihuahuanus coahuilae* (Williams, 1968), comb. nov., ♂ (AMNH). **B.** *Maaykuyak waueri* (Gertsch and Soleglad, 1972), comb. nov., ♂ (AMNH). Scale bars = 1 mm (**A**), 0.5 mm (**B**).

follows: *ib* and *it* are situated at PD6 in *Syntropis*, whereas *ib* is situated at or closer to PD6 and *it* is situated between PD5 and PD6 in *Kuarapu*, *Vizcaino*, gen. nov., and some species of *Paravaejovis*, such as *P. confusus*, comb. nov., and *P. waeringi*, comb. nov.

Syntropis shares with *Konetontli*, gen. nov., *Kuarapu*, *Maaykuyak*, gen. nov., *Vizcaino*, gen. nov., *Chihuahuanus bilineatus*, comb. nov., *C. coahuilae*, comb. nov., and *Thorellius cristimanus* the presence of a secondary hook on the hemispermatophore (fig. 8H), created by an extension of the axial carina of the distal lamina, that forms a pronounced bifurcation with the primary hook.

INCLUDED SPECIES: *Syntropis aalbui* Lowe et al., in Soleglad et al., 2007; *Syntropis macrura* Kraepelin, 1900; *Syntropis williamsi* Soleglad, Lowe, and Fet, 2007.

DISTRIBUTION: *Syntropis* is endemic to the Baja California Peninsula, Mexico, and recorded from the states of Baja California and Baja California Sur (fig. 4).

NATURAL HISTORY: Hjelle (1974) described the parturition and postparturition behavior of *Syntropis*. *Syntropis* species have been collected in rocky desert habitats, from sea level to 556 m altitude, with *S. aalbui* taken at the highest elevation. All three species of *Syntropis* are lithophilous, inhabiting the cracks and crevices of cliffs and rock walls, and hiding in loose rock piles or under exfoliating rock flakes. The habitat and habitus, particularly the slender, elongated pedipalps, legs, and metasoma, well-developed superciliary carinae of the medial ocular tubercle, and the tarsal morphology, are consistent with the lithophilous ecomorphotype (Prendini, 2001a). Jiménez-Jiménez and Pala-

cios-Cardiel (2010) reported capturing species in pitfall traps, indicating that these scorpions will disperse between rocky habitats. *Syntropis macrura* was reported to be synanthropic in the vicinity of the Comondús (Williams, 1980; Jiménez-Jiménez and Palacios-Cardiel, 2010) and observations suggest that population densities are greater at such oases.

MATERIAL EXAMINED: *Syntropis aalbui* Lowe et al., in Soleglad et al., 2007: **MEXICO: Baja California:** *Municipio de Ensenada*: Blue Palm Canyon (intermittent river La Bocana), 5 km N Cataviña, 13.vii.1979, R. Aalbu, holotype ♀ (MHNG). *Syntropis macrura* Kraepelin, 1900: **MEXICO: Baja California Sur:** *Municipio de Comondú*: San José Comondú, 27.viii.2006, C. Palacios, 1♂, 1♀ (CAECIB). *Syntropis williamsi* Soleglad, Lowe, and Fet, 2007: **MEXICO: Baja California Sur:** *Municipio de La Paz*: N of Los Aripes, 25.vi.1985, W.R. Lourenço and G.A. Polis, holotype ♀ (MHNG). *Municipio de La Paz*: El Pilar, ca. 20 km NE Las Pocitas, 24°28.7616′N 111°01.12′W, 92 m, 25.vi.2008, H. Montaño and E. González, 1♂, 1♀ (AMNH [ARA 2825]).

Thorellius Soleglad and Fet, 2008
Figures 1E, 5, 7, 17C, D, 20B, 21B; table 1

Vejovis intrepidus Thorell, 1876 [= *Thorellius intrepidus* (Thorell, 1876)], type species, by original designation.

Vejovis second section (part): Hoffmann, 1931: 134, 139.

Vaejovis second section (part): Francke and González-Santillán, 2007: 590.

Vaejovis intrepidus group (part): Sissom, 1989: 180; 1991: 24, 26; Stockwell, 1992: 409; Sissom, 1993: 68; Lourenço and Sissom, 2000: 135; Sissom, 2000: 537, 538, 551; Armas and Martín-Frías, 2001: 8; Hendrixson 2001: 47; González-Santillán, 2004: 30, 31; Ponce-Saavedra and Sissom, 2004: 539, 541; Graham and Fet, 2006: 7; McWest, 2009: 66, 69, 70, 100–102, table 1; Santibáñez-López and Sissom, 2010: 52.

Vaejovis punctipalpi group (part): Fet et al., 2006a: table 1; Soleglad and Fet, 2006: 6.

Thorellius Soleglad and Fet, 2008: 1, 95, 102 (part); Ayrey and Soleglad, 2011: 1 (part).

DIAGNOSIS: *Thorellius* may be separated from other genera of Syntropinae by the presence of nine fully developed retroventral macrosetae on the basitarsus of leg III (fig. 21B). Most of the other genera bear six or seven fully developed retroventral macrosetae, the other retroventral setae being smaller (McWest, 2009), whereas *Syntropis* has more than 10. The pedipalp patellar rlds and rlm carinae are weakly developed and smooth, the dorsal surface of the pedipalp femur finely and sparsely granular, and the ventral surface of the telson vesicle shagreened in all species of *Thorellius*.

Thorellius is most closely related to *Balsateres*, gen. nov., with which it shares broad pedipalpal and metasomal carinae. However, the carinae of *Thorellius* are moderately to densely granular, instead of smooth as in *Balsateres*, gen. nov. Both sexes of *Thorellius*, especially the female, exhibit a distinct proximal gap between the fixed and movable fingers, when closed, which is absent in *Balsateres*, gen. nov. The two genera also differ in base coloration and infuscation. *Thorellius* are dark and reddish in color, with various degrees of infuscation on the carapace and tergites, whereas *Balsateres*, gen. nov., is yellow and almost immaculate, except for the ocular tubercle, which is infuscate. *Thorellius intrepidus* (Thorell, 1876) shares with *Balsateres*, gen. nov., the presence of double basal prolateral denticles on the movable finger of the pedipalp chela (fig. 20A, B), but is readily separated from the latter by the densely granular carinae and intercarinal surfaces, which are smooth in *Balsateres*, gen. nov.

Species of *Thorellius* superficially resemble *Kochius*, but may be distinguished from the latter by the broad, raised pedipalp carinae, each comprising clustered granules (fig. 17C, D). The pedipalp carinae of *Kochius* are comparatively shallower and the granulation usually moniliform (fig. 18A, B). The two genera also differ in the macrosculpture of the vsm carinae of metasomal segments I–III, which are costate to weakly denticulate in *Thorellius* but granular in *Kochius*.

Thorellius contains the largest and most robust scorpions in the subfamily; the holotype of *T. intrepidus* is 94 mm in length (Sissom, 2000). *Syntropis*, the only genus with adults similar in total length, is comparatively slender, with narrow, elongated pedipalps, legs, and metasoma.

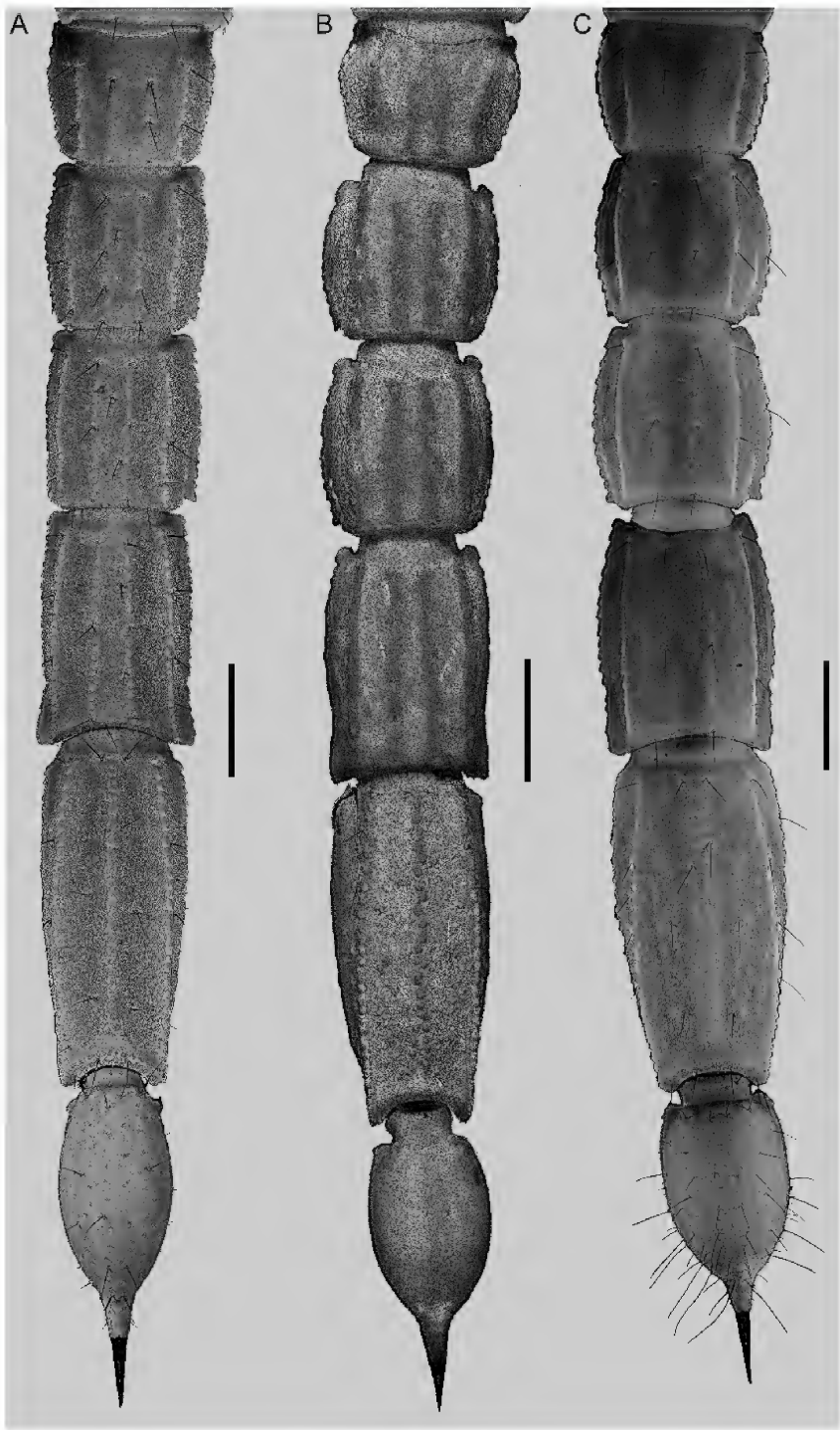


Fig. 27. Syntropinae Kraepelin, 1905, metasomal segments I–V and telson, ventral aspect, illustrating carinae. **A.** *Chihuahuanus coahuilae* (Williams, 1968), comb. nov., ♂ (AMNH). **B.** *Mesomexovis punctatus* (Karsch, 1879), comb. nov., ♂ (AMNH). **C.** *Paravaejovis diazi* (Williams, 1970), comb. nov., ♂ (AMNH). Scale bars = 2 mm.

INCLUDED SPECIES: *Thorellius atrox* (Hoffmann, 1931); *Thorellius cristimanus* (Pocock, 1898); *Thorellius intrepidus* (Thorell, 1876).

DISTRIBUTION: *Thorellius* is endemic to Mexico, and recorded from nine states on the mainland: Aguascalientes, Colima, Estado de México, Guanajuato, Guerrero, Jalisco, Michoacán, Nayarit, and Sinaloa (fig. 5). Hoffmann's (1931) records of *T. intrepidus* from Veracruz (Catemaco) on the eastern coast of Mexico are probably erroneous; extensive fieldwork has not yielded new collections from this area.

NATURAL HISTORY: There are relatively few data on the ecology of *Thorellius*. Species of the genus have mostly been collected on the surface at night with UV light detection or by turning stones during the day in subtropical deciduous forest from sea level to 1760 m altitude. As with *Mesomexovis*, gen. nov., *Thorellius* species are only active during the rainy season, and estivate during the dry season. Although González-Santillán (2004) suggested that *T. intrepidus* is pelophilous, the absence of fossorial adaptations suggests otherwise. The habitat and habitus of *Thorellius* are consistent with the lapidicolous ecomorphotype (Prendini, 2001a).

REMARKS: As redefined here, *Thorellius* accommodates a subset of species previously assigned to Hoffmann's (1931) "second section" of *Vaejovis*, later termed the *intrepidus* group by Sissom (1989), for which Soleglad and Fet (2008) devised the name *Thorellius*, without quantitatively testing its monophyly or composition. *Thorellius*, as defined by Soleglad and Fet (2008), was consistently polyphyletic, and the group of species hereby assigned to it consistently monophyletic, in the phylogenetic analyses of González-Santillán and Prendini (in press) based on morphology and those based on morphology and DNA. The following species are therefore transferred to other genera in the present contribution: *Balsateres cisnerosi*, comb. nov., previously assigned to *Thorellius* (Soleglad and Fet, 2008) and the *intrepidus* group (Santibáñez-López and Sissom, 2010); *Mesomexovis occidentalis*, comb. nov., and *Mesomexovis subcristatus*, comb. nov., previously assigned to the *intrepidus* group (Hoffmann, 1931; Sissom, 2000) and then to *Thorellius* (Soleglad and Fet, 2008).

MATERIAL EXAMINED: *Thorellius atrox* (Hoffmann, 1931): **MEXICO: Colima:** *Municipio de Colima*: Colima, in house, holotype ♂ of *Vaejovis intrepidus atrox* Hoffmann, 1931 (AMNH), 1♂, 1♀ paratypes (AMNH). *Thorellius cristimanus* (Pocock, 1898): **MEXICO: Colima:** *Municipio de Tonila*: Tonila, 3.2 km S, 28.viii.1965, W.J. Gertsch and R. Hastings, 1♂, 1♀ (AMNH). *Thorellius intrepidus* (Thorell, 1876): **MEXICO: Colima:** *Municipio de Armería*: Mine La Salada, NW Ixtlahuacan, 19°01.680′N 103°47.036′W, 275 m, Mine staff, 1♂, 1♀ (AMNH). *Municipio de Tecomán*: Tecomán, 18°54′30″N 103°52′28″W, 1♂, 1♀ (AMNH).

Vizcaino, gen. nov.

Figures 1F, 6, 7, 20C, 21C; table 1

Vejovis viscainensis Williams, 1970 [= *Vizcaino viscainensis* (Williams, 1970), comb. nov.], type species, by monotypy.

Vaejovis eusthenura group (part): Williams, 1980: 55; Sissom, 1991: 26; Stockwell, 1992: 408, 409; Sissom, 1993: 68; Lourenço and Sissom, 2000: 135; Sissom, 2000: 530, 532, 551; Armas and Martín-Frías, 2001: 8; González-Santillán, 2004: 29; Ponce-Saavedra and Sissom, 2004: 541; Francke and Ponce-Saavedra, 2005: 67; Sissom and Hendrixson, 2005b: 33, 34; Fet et al., 2006a: 7; 2006b: tables 1, 9; Graham and Soleglad, 2007: 9, 11, 12; Soleglad et al., 2007: 134, 135; McWest, 2009: 8, 48, 52, 56, 61, 64, 98, 101–103, 108, table 1; Santibáñez-López and Sissom, 2010: 49.

Hoffmannius (part): Soleglad and Fet, 2008: 1, 26, 57, 60, 89, 91, 96, 102; Ayrey and Soleglad, 2011: 1.

ETYMOLOGY: The generic name is a noun in apposition, masculine in gender, taken from the Vizcaino Desert in the Baja California Peninsula, to which this monotypic genus is endemic.

DIAGNOSIS: *Vizcaino*, gen. nov., is unique among Syntropinae in possessing four primary subrows of median denticles, separated by five retrolateral denticles, in the median denticle row of the pedipalp movable finger (fig. 20C); the terminal subrow, comprising one to three denticles in the other genera of Syntropinae, is absent (figs. 17A, C, 18A, 19A, C, 20A–C). The following combination of characters is also unique for the genus: pedipalp femur, rlv carina smooth and costate; legs I–III, basitarsi

(male and female) laterally compressed, each with dorsal and retrodorsal macrosetae elongated and arranged into a sublinear row, forming a setal comb (fig. 21C); legs I–IV, telotarsi each with basal, ventromedian and distal series of spinules slender and elongate (fig. 21C); metasomal segments I–IV, vsm carinae distinct (protruding above adjacent intercarinal surfaces) and finely denticulate.

Vizcaino, gen. nov., appears superficially similar to some species of *Chihuahuanus*, gen. nov., and *Paravaejovis* (e.g., *C. globosus*, comb. nov., *P. pumilis*, and, to a lesser extent, other species of *Paravaejovis* in the Baja California Peninsula) with which it shares setal combs on the basitarsi of legs I–III (fig. 21C). In addition to the above-mentioned characters, *Vizcaino*, gen. nov., differs from these taxa by possessing elongated pedipalp chela fingers, such that trichobothrium *eb* is situated on the fixed finger between RD6 and RD7, *it* is situated on the fixed finger between PD5 and PD6, and *ib* is situated on the fixed finger, at or close to PD6. Trichobothrium *eb* is situated at RD7, *it* at PD6 and *ib* between PD6 and PD7 in *Chihuahuanus*, gen. nov., and most species of *Paravaejovis*, except *P. confusus*, comb. nov., and related species in which the positions of these trichobothria are similar to those of *Vizcaino*, gen. nov. *Paravaejovis confusus*, comb. nov., and related species are readily distinguished from *Vizcaino*, gen. nov., by the dentition of the pedipalp chela movable finger, and the telotarsal spinules.

Vizcaino, gen. nov., shares with *Konetontli*, gen. nov., *Kuarapu*, *Maaykuyak*, gen. nov., *Syntropis*, *Chihuahuanus bilineatus*, comb. nov., *C. coahuilae*, comb. nov., and *Thorellius cristimanus* the presence of a secondary hook on the hemispermatophore (fig. 8H), created by an extension of the axial carina of the distal lamina, that forms a pronounced bifurcation with the primary hook.

INCLUDED SPECIES: *Vizcaino viscainensis* (Williams, 1970), comb. nov.

DISTRIBUTION: *Vizcaino*, gen. nov., is endemic to the Vizcaino Desert of the Baja California Peninsula, Mexico, and recorded from the states of Baja California and Baja California Sur (fig. 6).

NATURAL HISTORY: According to Williams (1970b), this species is rarely collected, and may have limited surface activity, spending most of its life inside burrows. The known specimens were collected at night with UV light detection on sparsely vegetated, semistabilized sand dunes, from sea level to 262 m altitude. This species appears to be more abundant in areas where coastal fog is frequent. The habitat and habitus, especially the setal combs and elongated spinules on the leg tarsi, and the pale, immaculate integument are consistent with the psammophilous ecomorphotype (Prendini, 2001a).

REMARKS: Williams (1980) originally placed this species in the *eusthenura* group of *Vaejovis*, for which Soleglad and Fet (2008) devised the name *Hoffmannius*, without quantitatively testing either its monophyly or composition. *Hoffmannius*, as defined by Soleglad and Fet (2008), was consistently polyphyletic in the phylogenetic analyses by González-Santillán and Prendini (in press). *Vizcaino*, gen. nov., was not related to the species assigned to *Hoffmannius* by Soleglad and Fet (2008), forming a monophyletic group with *Syntropis* instead (fig. 7). The creation of a monotypic genus for this species is based on its phylogenetic position and unique, diagnostic character combination.

MATERIAL EXAMINED: *Vizcaino viscainensis* (Williams, 1970), comb. nov.: **MEXICO: Baja California:** *Municipio de Ensenada*: Miller's Landing, 2 mi. NW, 25 ft, 21.vi.1968, S.C. Williams and M.A. Cazier, holotype ♂ of *V. viscainensis* (CAS Type No. 10429). **Baja California Sur:** *Municipio de Mulegé*: Las Bombas, 3.2 km E, 30 m, 16.iv.1969, S.C. Williams, 2♀ (AMNH); Sierra del Placer, 21 km to junction Bahía Tortugas and Bahía Asunción, 98 km E of Vizcaino towards Bahía Tortugas, 27°28.9278′N 114°17.0928′W, 262 m, 28.vi.2008, H. Montaño and E. González, 8♂, 6♀, 13 juv. (AMNH [ARA 2855]), 8♂, 6♀ (IBUNAM [ARA 2245]).

ON THE DISTRIBUTION AND DIVERSIFICATION OF SYNTROPINAE

The scorpion family Vaejovidae is the most diverse in North America. Most of this diversity is concentrated in Mexico and the southwestern United States (Lourenço and Sissom, 2000; Sissom and Hendrixson, 2005a). The Baja California Peninsula con-

Fig. 28. Syntropinae Kraepelin, 1905, metasomal segments I–V and telson, lateral aspect, illustrating carinae. **A.** *Balsateres cisnerosi* (Ponce-Saavedra and Sissom, 2004), comb. nov., ♂ (IBUNAM). **B.** *Konetontli acapulco* (Armas and Martín-Frías, 2004), comb. nov., holotype ♂ (IBUNAM). **C.** *Paravaejovis pumilis* (Williams, 1980), ♂ (AMNH). Scale bars = 2.5 mm (**A**), 1 mm (**B, C**).

tains 55 described species and the world's highest point diversity of scorpions (14 species per km^2 according to Polis, 1990). All except eight of these species are vaejovids.

Much of the species-level diversity in Vaejovidae falls within subfamily Syntropinae, distributed from Oregon and Utah in the southwestern United States to the Isthmus of Tehuantepec, in Chiapas and Oaxaca, Mexico. Six genera and 23 species of Syntropinae occur on the Baja California Peninsula and adjacent islands, two genera and 20 species of which are endemic. The vast arid region of the southwestern United States and northern Mexico, including the Chihuahuan, Great Basin, Mojave, and Sonoran (including Colorado) deserts, is less diverse in Syntropinae, containing four genera, all of which also occur in the Baja California Peninsula, and 15 species, all except one of which are endemic. Further southwest, members of the subfamily occupy most arid and subtropical lowland habitats along the Pacific coast, as well as the intermontane valleys of central mainland Mexico. Five genera and 16 species of Syntropinae inhabit this area, four genera and all species of which are endemic. There are no reliable records of Syntropinae from east of the Sierra Madre Oriental, along the coast of the Gulf of Mexico (table 1, figs. 3–6).

Although the distribution of the 11 genera of Syntropinae is mostly continuous, two genera present disjunct distributions: one species of *Konetontli*, gen. nov., occurs on the Baja California Peninsula and the other four are distributed along the Pacific coast of mainland Mexico, whereas the two species of *Maaykuyak*, gen. nov., occur on the peninsula and in the Chihuahuan Desert, respectively. These disjunct distributions can be explained by two major geological events: (1) the development of the Sierra Madre Occidental (SMOcc), ca. 34–27 Ma, and (2) the separation of the Baja California Peninsula from the mainland, ca. 12–5 Ma (Gastil et al., 1983). The presence of *Konetontli*, gen. nov., and *Maaykuyak*, gen. nov., in both areas suggests that their common ancestor predates the separation of the peninsula and, in the case of *Maaykuyak*, gen. nov., also the orogeny of the SMOcc. The basal phylogenetic position of the monophyletic group comprising *Konetontli*, gen. nov., and *Maaykuyak*, gen. nov., placed sister to all other Syntropinae (fig. 7), and followed by the monophyletic group comprising the two genera endemic to Baja California, *Syntropis* and *Vizcaino*, gen. nov., corroborates this hypothesis and suggests that these four genera are relictual.

The uplift of the Trans-Mexican Volcanic Belt (TMVB) during the Miocene, 5.3 Ma, created a formidable barrier for organisms distributed north to south across North America (Ortega-Gutiérrez and Guerrero-García, 1982; Ferrari et al., 2000; Ferrusquía-Villafranca and González-Guzmán, 2005), and especially those with limited vagility like scorpions (Polis, 1990; Prendini, 2001a). The development of the SMOcc likewise presented a barrier to organisms distributed west to east across the continent (Axelrod, 1979; Ortega-Gutiérrez and Guerrero-García, 1982). These events divided Mexico north and south of the TMVB, and subdivided the area north of the TMVB into the Chihuahuan and Sonoran deserts, respectively east and west of the SMOcc. Vicariance, induced by these geographical barriers, most likely promoted divergence between *Mesomexovis*, gen. nov., to the south of the TMVB, and the common ancestor of *Chihuahuanus*, gen. nov., and *Paravaejovis* to the north, the latter genera in turn diverging in the Chihuahuan and Sonoran deserts, after the development of the SMOcc. The relative timing of development of the above-mentioned geographical barriers and known distributions of these genera (figs. 3, 4, 6) match the phylogenetic relationships among them (González-Santillán and Prendini, in press; fig. 7).

The separation of the Baja California Peninsula from the North American mainland is among the primary forces driving the evolution and diversification of its endemic scorpion fauna including, among other taxa, two endemic and highly stenotopic genera of Syntropinae—the lithophilous *Syntropis*, comprising three known species, and the monotypic, psammophilous *Vizcaino*, gen. nov. Similarly, the Balsas Depression was separated from other tropical lowlands along the Gulf of Mexico by the orogeny of the TMVB and SMOcc (Ortega-Gutiérrez and Guerrero-García, 1982). Uplift of the Sierra

Madre del Sur in Oaxaca further sundered the connection with southern Mexico (Ortega-Gutiérrez and Guerrero-García, 1982). The extreme isolation of the Balsas Depression mirrors the isolation that occurred by the separation of the Baja California Peninsula in promoting the evolution of an endemic scorpion fauna including, among other taxa, two endemic and highly stenotopic genera of Syntropinae—the monotypic, lithophilous *Kuarapu* and the monotypic, psammophilous *Balsateres*, gen. nov.

The separation of the Baja California Peninsula appears to have also affected the evolution of the clade comprising *Kuarapu*, *Balsateres*, gen. nov., *Thorellius*, and *Kochius* (fig. 7). The ancestral distribution of these four genera probably extended throughout central and northern Mexico to the southwestern United States. Separation of the peninsula from the mainland created the presently disjunct distribution of *Kochius* by isolating one species, *K. sonorae*, on the mainland from the others, which diversified on the peninsula and in southern California.

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APPENDIX 1

Character List

List of 205 qualitative morphological characters scored for phylogenetic analyses of 61 species, representing 18 genera in the North American vaejovid scorpion subfamily Syntropinae Kraepelin, 1905 (González-Santillán and Prendini, in press). 45 quantitative morphological characters are excluded from this character list. Character states are scored 0–6, unknown (?) and inapplicable (-). Characters from previous matrices that correspond partially or entirely to those listed below are as follows: L80 (Lamoral, 1980); S89 (Stockwell, 1989); P00 (Prendini, 2000); FSB01 (Fet et al., 2001); S&S01 (Soleglad and Sissom, 2001); P03 (Prendini, 2003); PCW03 (Prendini et al., 2003); S&F03 (Soleglad and Fet, 2003); P04 (Prendini, 2004); FP08 (Francke and Prendini, 2008); VP08 (Volschenk and Prendini, 2008); PFV10 (Prendini et al., 2010).

Color and Infuscation

0. Cheliceral manus, dorsal surface, infuscation: immaculate, pale or nearly so (fingers may be slightly infuscate) (0); infuscate (1).
1. Carapace, base color (irrespective of infuscation): pale yellow or brownish-yellow (0); brown, orange-brown, or reddish-brown (1); dark brown or dark reddish-brown (2).
2. Carapace interocular surface (triangular area between median and lateral ocelli), infuscation: partially infuscate (0); immaculate (no infuscation) (1). [FSB01/9–11 (part); FP08/1]
3. Carapace circumocular surfaces, infuscation: infuscation not reaching lateral ocelli (0); immaculate (1). [FSB01/9–11 (part); FP08/2]
4. Carapace anterolateral surfaces, infuscation: infuscate (0); immaculate (1).
5. Carapace posterolateral and posteromedian surfaces, infuscation: infuscate (0); immaculate (1). [FSB01/9–11 (part); FP08/3]
6. Pedipalps, legs, tergites and metasoma, integument base color: pale (0); dark (1).
7. Pedipalp femur, dorsal intercarinal surfaces, infuscation: immaculate (0); infuscate (1).
8. Pedipalp patella, dorsal intercarinal surfaces, infuscation: immaculate to diffusely infuscate (0); markedly infuscate (1).
9. Pedipalp chela, color relative to femur and patella: similar (0); darker (1).
10. Pedipalp chela manus, intercarinal surfaces, infuscation: infuscate (0); immaculate (1). [FSB01/12 (part); FP08/5]
11. Pedipalp chela fingers, color relative to manus: darker (0); similar (pale or dark) (1). [FSB01/8; FP08/4]
12. Pedipalp chela fingers, infuscation: immaculate to diffusely infuscate (0); distinctly infuscate basally (1); entire finger infuscate (2).
13. Legs, color and infuscation: pale, immaculate to lightly infuscate (0); moderately infuscate (1); very dark, heavily infuscate (2).
14. Leg coxae, infuscation: immaculate (0); diffuse to moderately infuscate (1).
15. Tergites I–VII, dorsal median (dm) [= median] carina, infuscation, length (longitudinal development): no difference in infuscation from adjacent intercarinal surfaces (0); infuscation faintly or markedly darker than adjacent intercarinal surfaces: vestigial (restricted to proximal or distal margin of segment) (1); partial (not extending full length of segment) (2); complete (extending full length of segment) (3).
16. Tergites I–VII, intercarinal surfaces, infuscation: entirely infuscate (0); mostly infuscate, lateral and posterior margins immaculate (1); entirely or almost entirely immaculate (2). [FSB01/9 (part); FP08/6]
17. Sternites III–VI, intercarinal surfaces, infuscation: immaculate (0); finely infuscate laterally and around setae only (1); entirely infuscate (2).
18. Sternite VII, intercarinal surfaces, infuscation: immaculate (0); finely infuscate laterally and around setae only (1); entirely infuscate (2).
19. Metasomal segments I–IV, dorsal intercarinal surfaces, between dorsal lateral (dl) carinae, infuscation: immaculate (0); infuscate (1).
20. Metasomal segment V, dorsal intercarinal surfaces, between dl carinae, infuscation: immaculate (0); infuscate (1).
21. Metasomal segments I–IV, ventral intercarinal surfaces, infuscation: immaculate (0); infuscate (1). [FSB01/12 (part), 13; FP08/7]
22. Metasomal segment IV, color relative to segment III: similar (0); darker (1).
23. Metasomal segment V, color relative to segment IV: similar (0); darker (1).
24. Telson, color relative to metasomal segment V: paler (0); similar (1); darker (2).
25. Telson ventral surface, infuscation: immaculate (0); infuscate (1).

Chelicerae

26. Movable finger, distal denticles [prolateral and retrolateral distal teeth], relative size: subequal, distal external tooth slightly smaller than distal internal tooth (ventral > dorsal) (0); unequal, distal external tooth considerably smaller than distal internal tooth (ventral >> dorsal) (1). [L80/21 (part); P00/11; S&S01/1, 6; S&F03/31, 39; FP08/10]
27. Movable finger, distal denticles [prolateral and retrolateral distal teeth], alignment: opposable, distal internal tooth completely overlaps distal external tooth in dorsal aspect, creating deep U-shaped notch in anterior aspect (0); not opposable, distal internal tooth does not overlap or at most partially overlaps distal external tooth in dorsal aspect, creating shallow V-shaped notch in anterior aspect (1). [L80/21 (part); P00/11; S&S01/1, 6; S&F03/39; FP08/10; PFV10/4]
28. Movable finger, ventral edge, denticles: crenulate/1–7 small denticles (ventral accessory teeth sensu Stockwell, 1989) (0); smooth (1). [S89/34–36; S&S01/4; S&F03/42, 43]

29. Movable finger, ventral edge, serrula: present, well developed (0); present, reduced [vestigial] (1). [S89/37–39; S&S01/7; FP08/12]

Carapace Shape and Topography

30. Carapace anterior margin, curvature: concave (0); sublinear (1); convex (2). [FP08/14]
31. Carapace anteromedian (frontal) notch (emargination): obsolete [straight or subtle indentation] (0); present, shallow [shallow to medium indentation] (1). [S&S01/10; P00/3; FP08/14]
32. Carapace anteromedian longitudinal sulcus, anterior furcation: no furcation (0); furcation (1).
33. Carapace, median lateral sulci: pronounced/well developed (0); obsolete/indistinct (1).
34. Carapace, median ocular tubercle: raised (0); shallow (flat) (1).
35. Carapace, median ocular tubercle, superciliary carinae: higher than ocelli (0); lower than ocelli (1).

Carapace Ornamentation

36. Carapace interocular surface, texture: glabrous (smooth, shiny) (0); matte (uniformly finely granular) (1); shagreened (coarse granules on smooth or finely granular surface) (2).
37. Carapace interocular surface, texture, distribution: entirely glabrous (0); granular along median longitudinal and anterior furcated sulci only (1); frontal lobes and median surfaces granular, with glabrous areas (2); entirely granular (3).
38. Carapace anterolateral, median lateral, posterolateral, and posteromedian surfaces, texture: glabrous (0); matte (1); shagreened (2).

Pedipalp Carination

39. Femur, retrolateral dorsosubmedian (rlds) carina, ornamentation, texture and length: granular (includes costate-granular, i.e., confluent granules, e.g., crenulate, serrate or dentate), partial (0); granular, complete (1); smooth (includes costate), complete (2).
40. Femur, retrolateral ventral (rlv) carina, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2).
41. Femur, ventral retrolateral (vrl) carina, ornamentation, length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: vestigial (1); partial (2).
42. Femur, ventral retrosubmedian (vrs) carina, ornamentation, length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: vestigial (1); partial (2).
43. Femur, prolateral ventral (plv) [= internoventral] carina, ornamentation, length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: vestigial (1); partial (2).
44. Patella, dorsal retrolateral (drl) carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: smooth, vestigial (1); granular, complete (2); smooth, complete (3).
45. Patella, retrolateral dorsosubmedian (rlds) [= (dorsal) externomedian] carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular, vestigial (1); smooth, vestigial (2); granular, partial (3); granular, complete (4). [PFV10/44]
46. Patella, retrolateral median (rlm) [= (ventral) externomedian] carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular, vestigial (1); smooth, vestigial (2); granular, partial (3); granular, complete (4). [PFV10/45]
47. Patella, rlds and rlm carinae, relative development: rlm more strongly developed than rlds (0); rlds more strongly developed than rlm (1); rlm and rlds similarly developed (2).
48. Patella, rlds and rlm carinae, development relative to ventral retrolateral (vrl) carina: as strongly developed (0); less strongly developed (1).
49. Patella, ventral median (vm) carina, length: marginal tubercle only (0); vestigial (1); partial (2).
50. Patella, prolateral subdorsal (pls) carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: marginal tubercle only (1).
51. Patella, prolateral median (plm) [= (dorsal) internomedian = "dorsal patellar spur"] carina, length: vestigial (0); partial (1); complete (2). [S89/41, 42; S&F03/96; PFV10/43]
52. Patella, prolateral ventral (plv) [= (ventral) internomedian = "ventral patellar spur"] carina, landmark macroseta at distal margin, position relative to trichobothrium *i*: absent (-); approximately in line with trichobothrium (0); distal to trichobothrium (1).
53. Chela, dorsal prolateral (dpl) [= dorsal marginal (D4)] carina, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2).
54. Chela, dorsal median (dm) [= dorsal secondary (D3)] carina, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2). [P00/22; S&S01/24; PFV10/34]
55. Chela, dorsal retrosubmedian (drs) carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular, vestigial (1); granular, partial (2); granular, complete (3); smooth, complete (4).
56. Chela, dorsal retrosubmedian accessory (drsa) [= subdigital (D2)] carina, ornamentation, texture and length: no difference in height and/

or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: marginal tubercle only (1); granular, vestigial (2); smooth, vestigial (3). [S89/40; P00/19; S&S01/23; FP08/17 (part)]

57. Chela, dorsal retrolateral (drl) [= digital (D1)] carina, ornamentation, texture and length (longitudinal development): no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: smooth, partial (1); granular, complete (2); smooth, complete (3). [PFV10/35]
58. Chela, retrolateral dorsal (rld) carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular, partial (1); granular, complete (2) smooth, complete (3).
59. Chela, retrolateral median (rlm) [= external secondary (E)] and retrolateral ventrosubmedian (rlvs) carinae, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: smooth, vestigial (1); smooth, partial (2); granular, complete (3); smooth, complete (4). [PFV10/36]
60. Chela, retrolateral median (rlm) [= external secondary (E)] carina, development relative to dorsal retrolateral (drl) [= digital (D1)] carina and ventral retrolateral (vrl) [= ventroexternal (V1)] carina, if difference in height and/or texture from adjacent intercarinal surfaces: no difference in height and/or texture (-); difference in height and/or texture: similarly developed (0); less developed (1).
61. Chela, retrolateral subventral accessory (rlsa) carina, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2).
62. Chela, retrolateral subventral (rls) [= secondary accessory] and retrolateral subventral accessory (rlsa) carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2).
63. Chela, retrolateral subventral (rls) [= secondary accessory] carina, ornamentation, connection to ventral retrolateral (vrl) [= ventroexternal (V1)] carina, if difference in height and/or texture from adjacent intercarinal surfaces: no difference in height and/or texture (-); difference in height and/or texture: rls and vrl carinae connected, continuous to external movable finger condyle (0); rls disconnected from vrl carina, discontinuous (1). [P00/27; S&S01/25]
64. Chela, retrolateral ventral (rlv) carina, ornamentation, length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: vestigial (1); partial (2).
65. Chela, ventral retrolateral (vrl) [= ventroexternal (V1)] carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular, complete (1); smooth, complete (2).
66. Chela, ventral retrosubmedian (vrs) carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular, vestigial (1); granular, partial (2); granular, complete (3) smooth, complete (4).
67. Chela, ventral median (vm) [= ventrointernal (V2)] carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular, vestigial (1); smooth, vestigial (2); granular, complete (3); smooth, complete (4). [P00/28; S&S01/26; FP08/18; PFV10/38, 39]
68. Chela, ventral prosubmedian (vps) [= V2] carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: smooth, vestigial (1); granular, complete (2); smooth, complete (3).
69. Chela, ventral prolateral (vpl) carina, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2).
70. Chela, ventral prolateral (vpl) + prolateral ventral (plv) [= ventral internal (V3/I)] and prolateral ventrosubmedian (plvs) + prolateral median (plm) [= dorsal internal (D5)] carinae, relative development: vpl + plv more strongly developed (0); vpl + plv and plvs + plm similarly developed (1); plvs + plm more strongly developed (2).
71. Chela, prolateral dorsal (pld) carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: smooth, vestigial (1); granular, partial (2); smooth, partial (3); granular, complete (4).
72. Chela, prolateral median (plm) [= dorsointernal (D5)] carina, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2).
73. Chela, prolateral ventrosubmedian (plvs) carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular, vestigial (1); granular, complete (2); smooth, complete (3).
74. Chela, prolateral ventral (plv) [= internomedian (V3/I)] carina, ornamentation, texture and length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular, vestigial (1); granular, complete (2); smooth, complete (3).

Pedipalp Surface Ornamentation

75. Femur, dorsal intercarinal surfaces, ornamentation, texture: glabrous (0); matte (1); shagreened (2); unevenly (non-uniform) finely granular (3).

76. Femur, ventral intercarinal surfaces, ornamentation, texture: glabrous (0); matte (1); shagreened (2).
77. Patella, prolateral intercarinal surfaces, ornamentation, texture: glabrous (0); matte (1); shagreened (2).
78. Patella, dorsal intercarinal surfaces, ornamentation, texture: glabrous (0); matte (1).
79. Patella, retrolateral intercarinal surfaces, ornamentation, texture: glabrous (0); matte (1); shagreened (2).
80. Patella, ventral intercarinal surfaces, ornamentation, texture: glabrous (0); matte (1); shagreened (2).
81. Chela, ventral intercarinal surfaces (between "V1" and "V2" carinae), ornamentation, texture: glabrous (0); matte (1); shagreened (2).

Pedipalp Shape

82. Patella, dorsal intercarinal surface, curvature, relative to dorsal prolateral (dpl) [= dorsal marginal (D4)] and dorsal retrolateral (drl) [= digital (D1)] carinae: flat, level with or slightly ventral to dpl and drl carinae (0); concave, inclined to medial aspect of segment below dpl and drl carinae (1).
83. Chela manus, shape: flat, angle "D1":"D3":"D4" carinae = 180° [flat/hexagonal or vaulted] and angle "V1":"V2":"V3" carinae = 180° [flat/hexagonal] (0); obtuse, angle "D1":"D3":"D4" carinae > 90° < 180° and angle "V1":"V2":"V3" carinae > 90° < 180° [rounded] (1). [S&S01/21, 22; S&F03/93]
84. Chela manus, shape: planes "D1"|"D4" carinae and "V1"|"V3" carinae nonparallel, distance between "D1"|"V1" carinae < "D4"|"V3" carinae (0); planes "D1"|"D4" carinae and "V1"|"V3" carinae parallel, distance between "D1"|"V1" carinae = "D4"|"V3" carinae (1). [S&S01/21; S&F03/93]
85. Chela manus, depression between dorsal prolateral (dpl) + dorsal prosubmedian (dps) [= dorsal marginal (D4)] carinae and dorsal median (dm) + dorsal retrosubmedian (drs) [= dorsal secondary (D3)] carinae at proximal margin, in prolateral view: absent or very shallow (0); deep (1).

Pedipalp Chela Finger Lobes and Notches

86. Chela fingers, closure [gap] (♂): fingers fit together evenly, gap absent or minimal when closed (0); fingers fit together unevenly, distinct gap evident when closed (1).
87. Chela fingers, closure [gap] (♀): fingers fit together evenly, gap absent when closed (0); fingers fit together unevenly, distinct gap evident when closed (1). [PFV10/31]
88. Chela fixed finger dentate margin, basal/proximal notch (PN) (♂): sublinear (0); emarginate, shallow notch (1); emarginate, moderate to deep notch (2).
89. Chela fixed finger, dentate margin, PN (♀): sublinear (0); emarginate, shallow notch (1).
90. Chela fixed finger, dentate margin, median lobe (ML) (♂): sublinear (0); weak to moderate lobe (1); strong lobe (2) unknown (?).
91. Chela fixed finger, dentate margin, ML (♀): sublinear (0); weak lobe (1); unknown (?).
92. Chela movable finger dentate margin, PN (♂): sublinear (0); emarginate, moderate to deep notch (1).
93. Chela movable finger, dentate margin, ML (♂): sublinear (0); weak to moderate lobe (1); strong lobe (2); unknown (?). [P00/35; P03/29; PCW03/25 (part); P04/4; VP08/13]
94. Chela movable finger dentate margin, median notch (MN) (♂, ♀): sublinear (0); emarginate, moderate to deep notch (1).
95. Chela fingertips: distinct whitish sensory surface (0); unmodified plain, smooth, elevated area (1).

Pedipalp Finger Dentition

96. Chela fixed and movable fingers, terminal denticle: considerably larger than preceding denticles, hooklike (0); slightly larger than preceding denticles (1). [PFV10/29]
97. Chela fixed and movable fingers, median denticle row, denticle development: denticles unmodified (0); denticles flat, elongated and pointed, forming serrated cutting edge (sensu Soleglad and Sissom, 2001) (1).
98. Chela fixed finger, median denticle row, primary subrows and retrolateral denticles (RD), count: 3 (0); 5 (1); 6 (2).
99. Chela fixed finger, prolateral denticles (PD), count: 4 (0); 5 (1); 6 (2); 8 or more (3). [FP08/20; S&S01/33]
100. Chela movable finger, median denticle row, primary subrows and retrolateral denticles (RD), count: 4 (0); 5 (1); 6 (2); 7 (3). [S&S01/33; S&F03/55; P04/6]
101. Chela movable finger, median denticle row, first (terminal) primary subrow: absent (no denticles) (0); one (occasionally two) denticles (1); usually three or more denticles (2). [S&F03/55; P04/6; PFV10/16]
102. Chela movable finger, PD6: present (0); absent (1). [S&S01/33; PFV10/22]
103. Chela movable finger, PD8: present (0); absent (1). [S&S01/33; PFV10/24]
104. Chela movable finger, prolateral accessory denticles (PAD) (supernumerary granules sensu Sissom, 1990): absent (0); numerous, irregularly positioned PAD, variable in number and position (1). [S&S01/29, 33; S&F03/49, 52; FP08/21]

Pedipalp Trichobothria

105. Femur, trichobothrium *d*, position relative to trichobothrium *i*: proximal or aligned (0); distal (1). [S&S01/38; S&F03/5]
106. Patella, external surface, distance trichobothria esb_1–esb_2 relative to distance trichobothria em_1–em_2: less than or equal (0); considerably greater than (1). [S&F03/29]
107. Patella, ventral surface, trichobothrium v_2, position relative to trichobothria v_1 and v_3:

approximately equidistant between v_1 and v_3 (0); closer to v_1, distance v_2–v_3 > distance v_1–v_2 (1). [S&F03/27]

108. Chela manus, trichobothrium *Db*, position relative to drl [D1] carina: ventral (0); on carina (1); dorsal (2). [S89/81, 83–85; P00/51, 52; S&F03/19; FP08/29]
109. Chela manus, trichobothrium *Dt*, position: proximal third (0); medial third (1). [S89/81, 83–85; P00/52; S&F03/19]
110. Chela manus, trichobothrium Eb_1, position: retrolateral surface (0); on vrl [V1] carina (1). [S&S01/45; S&F03/8]
111. Chela manus, external surface, trichobothrium Et_4, position relative to trichobothrium Et_3: aligned (0); distal (1).
112. Chela, trichobothrium Et_5, position: manus, posterior to articulation between fixed and movable fingers, near trichobothrium Et_4 (0); at base of fixed finger, aligned with or distal to articulation, removed from Et_4 (1). [S&F03/15, 22; FP08/34]
113. Chela manus, ventral surface, trichobothria, count: 4 (no accessory trichobothria) (0); 9 or more (5 or more accessory trichobothria) (1). [L80/14; S89/75, 76; P00/49; FSB01/5; S&S01/57; S&F03/32; FP08/36]
114. Chela, manus, ventral surface, trichobothrium V_3, position: proximal third (0); medial third (1).
115. Chela, manus, trichobothrium V_4, position: ventral surface (0); on vrl [V1] carina or retrolateral surface (1). [S89/80; S&S01/43; S&F03/7]
116. Chela, retrolateral surface, trichobothrium *db*, position: manus or base of fixed finger, not distal to articulation between fixed and movable fingers (0); proximal third of fixed finger, distal to articulation (1). [S&S01/66]
117. Chela fixed finger, retrolateral surface, trichobothrium *eb*, position: base of fixed finger, near articulation between fixed and movable fingers (0); proximal third of fixed finger (1); medial to distal third of fixed finger (2). [P00/61; FP08/43]
118. Chela fixed finger, retrolateral surface, trichobothrium *esb*, position: between RD6 and articulation with movable finger, but closer to articulation (0); midway between RD6 and articulation (1); at or close to RD6 (2); between RD5 and RD6 (3); at or close to RD4 (4) [RD numbering starts at terminal denticle; RD refers to denticle and/or associated macroseta].
119. Chela fixed finger, retrolateral surface, trichobothrium *est*, position: between RD3 and RD4 (0); between RD4 and RD5 (1); between RD5 and RD6 (2).
120. Chela fixed finger, retrolateral surface, trichobothrium *et*, position: between RD2 and RD3 (0); between RD3 and RD4, at or closer to RD3 (1); midway between RD3 and RD4 (2); between RD3 and RD4, at or closer to RD4 (3).
121. Chela fixed finger, prolateral surface, trichobothrium *ib*, position: proximal to RD7 (0); at or close to RD7 (1); between RD6 and RD7 (2); at or close to RD6 (3); between RD5 and RD6 (4); at or close to RD5 (5). [S89/71–72; P00/48; S&S01/40, 41; S&F03/10; FP08/44]
122. Chela fixed finger, prolateral surface, trichobothrium *it*, position: proximal to RD7 (0); at or close to RD7 (1); between RD6 and RD7 (2); at or close to RD6 (3); between RD5 and RD6 (4); at or close to RD5 (5); between RD4 and RD5 (6). [S89/70–72; P00/47; S&S01/40, 41; S&F03/11, 14; FP08/45]

Leg Proportions and Ornamentation

123. Legs II and IV, coxa proportions (anterior lengths IV/II): 1.3–2.0 (0); 2.2–2.9 (1). [S&F03/72]
124. Legs I–IV, femora, prolateral surfaces, texture: glabrous to unevenly (non-uniform) granular (0); matte (1); shagreened (2).

Leg Setation

125. Legs I and II, basitarsi, setal combs (♂): absent, dorsal and retrodorsal setae arranged into two separate parallel to subparallel rows ("distal plus proximal subrows" according to Haradon, 1985: 23, table 1) (0); present, dorsal and retrodorsal setae arranged into single sublinear to linear row ("single continuous row" according to Haradon, 1985: 23, table 1) (1).
126. Legs I and II, basitarsi, setal combs (♀): absent, dorsal and retrodorsal setae arranged into two separate parallel to subparallel rows (0); present, dorsal and retrodorsal setae arranged into single sublinear to linear row (1).
127. Leg III, basitarsus, setal combs (♂, ♀): absent, dorsal and retrodorsal setae arranged into two separate parallel to subparallel rows (0); present, dorsal and retrodorsal setae arranged into single sublinear to linear row (1).
128. Leg III, basitarsus, retroventral series, macroseta 8 (RV series of McWest, 2009: 8): present (0); absent (1).
129. Leg III, basitarsus, retroventral series, macroseta 9 (RV series of McWest, 2009: 8): present (0); absent (1).
130. Leg III, basitarsus, ventral series, macroseta 5 (DV of McWest, 2009: 8): present (0); absent (1).
131. Leg III, basitarsus, ventral series, macroseta 6 (DV of McWest, 2009: 8): present (0); absent (1).
132. Leg I, telotarsus, proventral macrosetae, count: 2 (0); 3 (1); 4 (2).
133. Leg I, telotarsus, retroventral macrosetae, count: 2 (0); 3 (1); 4 (2).
134. Legs II and III, telotarsi, proventral macrosetae, count: 2 (0); 3 (1); 4 (2).
135. Leg II, telotarsus, retroventral macrosetae, count: 2 (0); 3 (1); 4 (2).
136. Leg III, telotarsus, retroventral macrosetae, count: 2 (0); 3 (1); 4 (2).
137. Leg IV, telotarsus, proventral macrosetae, count: 3 (0); 4 (1).
138. Leg IV, telotarsus, retroventral macrosetae, count: 2 (0); 3 (1); 4 (2).

Leg Spinules

139. Legs I–IV, basitarsi and telotarsi, ventral surfaces, spinules, type: stout (0); slender,

elongate (1); bristlelike (2). [L80/9; S89/93, 94, 97; P00/68, 70; S&S01/83, 84, 88, 89; S&F03/57, 58; FP08/48; PFV10/153]

140. Leg III, basitarsus, retroventral spinules: distal spinules only (0); short distal row (1); long, partial row (2); long, complete row (3). [S&S01/85]
141. Leg IV, basitarsus, retrolateral spinules: distal spinules only (0); row of scattered spinules (1). [S&S01/85]
142. Legs I–IV, telotarsi, ventral surface, spinules, proximal row, configuration: curved/arc-shaped (0); loop or cluster (1). [PFV10/149]
143. Legs I–IV, telotarsi, ventral surface, spinules, ventrodistal pairs (VDS sensu McWest, 2009), count: 1 (0); 2 (1); 3 or 4 (2). [S89/97 (part), 100; S&S01/83; S&F03/62; PFV10/151]

Genital Operculum

144. Genital operculum, sclerites (♀): separated for most of length, loosely connected at anterior edge (0); partially fused, separated at posterior 20–25% of their length, connected to mesosoma in anterior half (1); partially fused, separated at posterior 20–25% of their length, connected to mesosoma in anterior third (2); fused, strongly connected by membrane entire length, with clear median suture (3). [L80/12 (part); S89/105–107; P00/80; S&F03/82; FP08/52]
145. Genital opercula, hinge of sclerites (♀): sclerites unable to open as a distinct "flap" (0); sclerites able to open as single, distinct "flap" (1).

Hemispermatophore

146. Hemispermatophore, sperm duct, floor: bearing greatly reduced, pouchlike invagination (0); bearing enlarged, pouchlike invagination (1). [S89/116]
147. Hemispermatophore, sclerotized hemimating/sperm plug, type I (derived from inner lobe): not developed (0); greatly reduced (inner lobe small) (1); fully developed (inner lobe large, tapered) (2).
148. Hemispermatophore, sclerotized hemimating/sperm plug, type I, distal barb margin: smooth (0); spinose (armed with spines, hooks or teeth) (1). [S89/119]
149. Hemispermatophore, sclerotized hemimating plug, type II (derived from floor of sperm duct): smooth (0); spinose (1).
150. Hemispermatophore, "dorsal trough margin" sensu Sissom (1991) (carina) and "ventral trough margin" (carina), terminal spinelike processes: fused into sclerotized crest or lobe (0); fused into prominent, often bifurcated hook (1). [L80/13; P00/90; S&F03/80]
151. Hemispermatophore, "dorsal trough margin" (carina), shape: short, broad, curving proximally, moderate distance to ventral trough margin (0); long, narrow, curving proximally, large distance to ventral trough margin (1).
152. Hemispermatophore, laminar "hooks," lobes and homologous structures derived from terminal spinelike processes of "dorsal trough margin" (carina) and "ventral trough margin" (carina), position: on dorsal/ectal surface (0); on lamina (ental/dorsal) margin (1).
153. Hemispermatophore, laminar "hooks," lobes and homologous structures derived from terminal spinelike processes of "dorsal trough margin" (carina) and "ventral trough margin" (carina), position on lamina: basal (0); distal ("elevated") (1).
154. Hemispermatophore, secondary hook created by extension of axial carina (sensu Lamoral, 1979): no secondary hook on distal lamina (axial carina completely fused to trough margins, no groove visible, i.e., "intact" sensu Soleglad and Fet, 2008) (0); basal on lamina (ental/dorsal) margin or on dorsal/ectal surface, weakly developed hook created by fusion of trough margins (axial carina partially fused to trough margins, forming shallow notch with visible "groove") (1); basal on lamina (ental/dorsal) margin or on dorsal/ectal surface, well developed hook near primary hook created by fusion of trough margins (axial carina separate from trough margins, forming deep notch, i.e., "bifurcate") (2); basal on lamina margin, fused with primary hook to create "flange" (3); distal on lamina margin, separated from primary hook or flange (4).
155. Hemispermatophore, distal lamina, dorsal/ental margin: straight (0); curved to ectal/dorsal surface, creating "inflection point" ("internal protuberance" sensu Soleglad and Fet, 2008) (1).
156. Hemispermatophore, distal lamina, shape: unconstricted (0); basally constricted (1). [S&S01/76]
157. Hemispermatophore, distal lamina, shape: even width almost to tip (0); broad near base, tapered to tip (1). [S&S01/78; S&F03/79]
158. Hemispermatophore, distal lamina, distal/apical crest (carina): not developed (0); distinct (1).

Pectines

159. Pectines, length relative to length of leg IV coxa (♂): long, distal edge reaching beyond distal edge of coxa (0); moderate, distal edge reaching to, but not beyond, distal edge of coxa (1). [S&F03/103; PFV10/170]
160. Pectines, length relative to length of leg IV coxa (♀): long, distal edge reaching beyond distal edge of coxa (0); moderate, distal edge reaching to, but not beyond, distal edge of coxa (1); short, distal edge not reaching to distal edge of coxa (2). [S&F03/103; PFV10/171]
161. Pectines, first proximal median lamella (scape), angle (♂): acute, $< 90°$ (0); approximately 90° (1); obtuse, $> 90°$ but $< 180°$ (2). [PFV10/169]
162. Pectines, first proximal median lamella (scape), angle (♀): approximately 90° (0); obtuse, $> 90°$ but $< 180°$ (1); straight or shallowly curved, approximately 180° (2).
163. Pectines, first (proximal/basal) pectinal tooth (♀): unmodified, similar to subsequent teeth, sensilla field present (0); modified, usually rounded in shape and often larger than subsequent teeth, sensilla field absent (1). [P04/12]

Mesosomal Carination

164. Tergites I–VI, dorsal lateral anterior/posterior (dl a/p) [= dorsosubmedian] carinae, ornamentation, length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: vestigial (restricted to anterior or posterior margin of segment) (1).
165. Sternite VII, ventral submedian (vsm) carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1).
166. Sternite VII, ventral lateral (vl) carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2). [PFV10/176]

Mesosomal Surface Ornamentation

167. Tergites I–VII (posttergites), intercarinal surfaces, texture: glabrous (0); matte (1); sparsely shagreened (2); densely shagreened (3).
168. Sternites III–VI, median surfaces, texture: glabrous (0); matte (1).
169. Sternite V, posteromedian surface, glandular area (♂): unmodified (0); smooth, raised area (1). [PFV10/175]
170. Sternite VII, median intercarinal surface, texture: glabrous (0); matte (1); shagreened (2).
171. Sternite VII, lateral intercarinal surfaces, texture: glabrous (0); matte (1); shagreened (2).
172. Sternite VII, glandular area (♂): unmodified or obsolete (very reduced, flat white spot posteromedially) (0); distinct raised, whitish triangular boss, restricted to posteromedial third of segment (1); distinct flat, whitish glandular area between ventrosubmedian carinae, extending almost entire length of segment (2).

Metasomal Carination

173. Metasomal segments I–IV, dorsal lateral anterior/posterior (dl a/p) [= dorsosubmedian/dorsal] carinae, ornamentation, texture: granular (0); smooth (1). [PFV10/178, 180]
174. Metasomal segment V, dl a/p [= dorsolateral] carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: smooth (1). [PFV10/183]
175. Metasomal segments I–III, lateral median anterior/posterior (lm a/p) [= dorsolateral] carinae, ornamentation, texture: granular (0); smooth (1). [PFV10/181]
176. Metasomal segment IV, lm a/p [= dorsolateral] carinae, ornamentation, texture: granular (0); smooth (1). [PFV10/182]
177. Metasomal segments I–IV, dl a/p (I–III or I–IV) and lm a/p (I–IV), distal granules, size relative to preceding granules: not noticeably larger (0); significantly larger and spiniform (1). [PFV10/179]
178. Metasomal segment V, lm a/p [= median lateral] carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2).
179. Metasomal segment V, lm a/p carinae, ornamentation, length: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: partial (1). [S&F03/86]
180. Metasomal segment I, lateral inframedian (lim) [= median lateral] carinae, ornamentation, texture: granular (0); smooth (1).
181. Metasomal segments II and III, lim carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2).
182. Metasomal segment IV, lim carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1).
183. Metasomal segment I, lim carinae, ornamentation, length: partial (0); complete (1). [PFV10/186]
184. Metasomal segment II, lim carinae, ornamentation, length: vestigial (0); partial (1). [PFV10/187]
185. Metasomal segment III, lim carinae, ornamentation, length: vestigial (0); partial (1). [PFV10/188]
186. Metasomal segments I–IV, ventral lateral (vl) carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2). [PFV10/189, 190]
187. Metasomal segment V, vl carinae, ornamentation, texture: granular (0); smooth (1). [PFV10/191]
188. Metasomal segment V, vl carinae, ornamentation, length: vestigial (0); complete (1). [PFV10/192]
189. Metasomal segment I, ventral submedian (vsm) carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2).
190. Metasomal segment II, vsm carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2). [S89/132, 133; P00/95; S&S01/12; S&F03/85]
191. Metasomal segment III, vsm carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2). [S89/132, 133; P00/95; S&S01/12; S&F03/85]
192. Metasomal segment IV, vsm carinae, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1); smooth (2). [S89/132, 133; P00/95; S&S01/12; S&F03/85]
193. Metasomal segment V, ventral median (vm) carina, ornamentation, texture: no difference in height and/or texture from adjacent intercarinal surfaces (0); difference in height and/or texture: granular (1). [S&F03/84]

Metasomal Surface Ornamentation

194. Metasomal segments I–III, lateral intercarinal surfaces (between dsl and vl carinae), texture: glabrous (0); matte (1); shagreened (2).

195. Metasomal segments IV and V, lateral intercarinal surfaces, texture: glabrous (0); matte (1); shagreened (2).
196. Metasomal segments I–IV, ventral intercarinal surfaces (between vl carinae), texture: glabrous (0); matte (1).
197. Metasomal segment V, ventral intercarinal surfaces, texture: glabrous (0); matte (1); shagreened (2).

Telson

198. Vesicle, macrosetae, length relative to aculeus (♂): moderate, shorter than aculeus (0); elongate, some as long as or longer than aculeus (1).
199. Vesicle, macrosetae, length relative to aculeus (♀): moderate, shorter than aculeus (0); elongate, some as long as or longer than aculeus (1).
200. Vesicle, dorsal surface, glands (♂): absent (surface unmodified) (0); small to medium-sized fusiform, whitish glandular area anterior to base of aculeus (1); medium-sized oval, whitish glandular area medially on dorsal surface (2). [FSB01/14; FP08/61]
201. Vesicle, ventral surfaces, texture: glabrous to matte (0); shagreened (1).
202. Subaculear tubercle: absent (0); laterally compressed, triangular tooth or spiniform conical tubercle with blunt tip (1); spiniform tooth or conical tubercle with sharp tip (2). [L80/15; S89/135; P00/106; P04/27; S&F03/90]
203. Compound subaculear tubercle: absent (0); single laterally compressed, triangular tooth or spiniform conical tubercle with blunt tip (0); multiple laterally compressed, triangular teeth or spiniform conical tubercles along medial axis of vesicle (1).
204. Aculeus, base, lateral microserration ("spicules" sensu Lamoral, 1979; "laterobasal serrations" sensu Fet et al., 2006a) (♂): absent (surface unmodified) (0); present (1).